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Colour frontispiece: Caption C refers to Figure D.
Caption D refers to Figure C.

p. 283, Insert after 1st paragraph, Column 2: **Distribution.** Japan, South China Sea, north-western Australia to Queensland, Lord Howe Island, Malaysia, 55–270 m.

p. 330, 2nd column, ref. Wicksten & Mendez, last line read: the Eastern Pacific Ocean. Bulletin of the Southern California Academy of Sciences 8(3): 106–120.

p. 333, 1st column, line 4, Barker & Grigg, 1977 read: Grigg & Barker, 1977

p. 334, 1st column, line 17, Barker & Grigg, 1977 read: Grigg & Barker, 1977

p. 337, References, reference 2, Barker & Grigg, 1977 read: Grigg & Barker, 1977

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p. 343, figure caption Figure 5 refers to Figure 6 (p. 344)

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NATURAL HISTORY

A Review of the Scincid Lizards of New Caledonia

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ABSTRACT. This monograph reviews the alpha taxonomy of the scincid lizards of New Caledonia (excluding the Loyalty Islands group). It also touches on the beta taxonomy of the species where possible but leaves much of this problem to a future review of phylogenetic relationships of the Lygosomine lineage of which New Caledonian species are a part. The following 10 genera including 24 species are recognized: *Geoscincus* n. gen.: *G. haraldmeieri* (Böhme); *Phoboscincus* Greer, 1974: *P. bocourti* (Brocchi), *P. garnieri* (Bavay); *Graciliscincus* n. gen.: *G. shonae* n. sp.; *Leiolopisma* Duméril & Bibron, 1839: *L. nigrofasciolatum* (Peters), *L. greeri* Böhme, *L.steindachneri* (Bocage), *L. novaecaledoniae* (Parker); *Tropidoscincus* Bocage, 1873: *T. variabilis* (Bavay), *T. aubrianus* Bocage, *T. rohssii* (Anderson); *Marmorosphax* n. gen.: *M. tricolor* (Bavay), *M. euryotis* (Werner); *Caledoniscincus* n. gen.: *C. austrocaledonicus* (Bavay), *C. atropunctatus* (Roux), *C. festivus* (Roux), *C. orestes* n. sp.; *Sigaloseps* n. gen.: *S. deplanchei* (Bavay); *Cryptoblepharus* Weigmann, 1834: *C. novocaledonicus* Mertens; *Nannoscincus* Günther, 1872: *N. mariei* (Bavay), *N. gracilis* (Bavay), *N. sleveni* (Loveridge), *N. rankini* n. sp., *N. greeri* n. sp. Most of the recognised species are endemic to the main island and most are confined to rainforest habitats. Some also occur on adjacent offshore islands. Generic accounts contain synonomies, diagnostic features and lists of species included. Keys are provided for monophyletic genera with more than two species. Species accounts contain data on synonomies, diagnostic features, types, morphology, habits, distribution, historical and taxonomic remarks, and specimens examined.

SADLIER, ROSS A., 1987. A review of the scincid lizards of New Caledonia. Records of the Australian Museum 39(1): 1-66.

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The territory of New Caledonia is located in the south-west Pacific (19–23°S latitude and 163–168°E longitude), and consists of the large main island of approximately 16,000 square kilometres, the Isle of Pines, the Huon Islands and the Loyalty Islands. A chain of mountains extending along its centre effectively divides the main island into a moist east coast, thickly forested for most its length, and a relatively dry, sparsely wooded west coast. Habitats typical of those occurring along the east and northern coast, and on the eastern and western ranges are shown in Fig. 1.

The endemic taxa include all known species of *Geoscincus, Graciliscincus, Marmorosphax, Tropidoscincus, Sigaloseps,* all New Caledonian *Nannoscincus,* three of the four New Caledonian *Leiolopisma (L. greeri, L. steindachneri, L. novacaledoniae),* and two of four of the currently recognised species of *Caledoniscincus (C. festivus, C. orestes).* Four species (*C. atropunctatus, C. austrocaledonicus, L. nigrofasciolatum, C. novocaledonicus)* in addition to being found on the main and offshore islands of New Caledonian also occur on islands of the Loyalty Island group, and one species (*C. atropunctatus)* is also recorded from Vanuatu.

Most species endemic to the main island are confined to rainforest habitat (except species of *Tropidoscincus).* Of the endemic taxa, four species (*T. rohssii, S. deplanchei, N. mariei, G. shonae)* occur largely in the south of the island over an area approximately covering that of the serpentine region of rock outcropping.

In 1978 the late Peter R. Rankin and I undertook fieldwork on the main island and made a large lizard collection before Peter died in a collecting accident. One of the ultimate aims of making these collections was a revision of the lizard fauna of New Caledonia the first part of which is here presented as a monograph on the scincid lizards of the main and immediately adjacent offshore islands. This work is dedicated to the memory of Peter Rankin.

Abbreviations

Institutional acronyms used in this paper are given below.

AM	Australian Museum, Sydney
BM	British Museum (Natural History), London
CAS	California Academy of Sciences, San Francisco
MCZ	Museum of Comparative Zoology — Harvard University, Cambridge
MNHP	Muséum National d'Histoire Naturelle, Paris
MRHN	Institute Royal des Sciences Naturelles de Belgique, Brussels
NHMB	Naturhistorisches Museum, Basel
NHMG	Naturhistoriska Museet, Göteburg
QM	Queensland Museum, Brisbane
SMF	Natur-Museum und Forschungs-Institut, Senckenberg
ZFMK	Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn
ZMB	Zoologisches Museum, Berlin

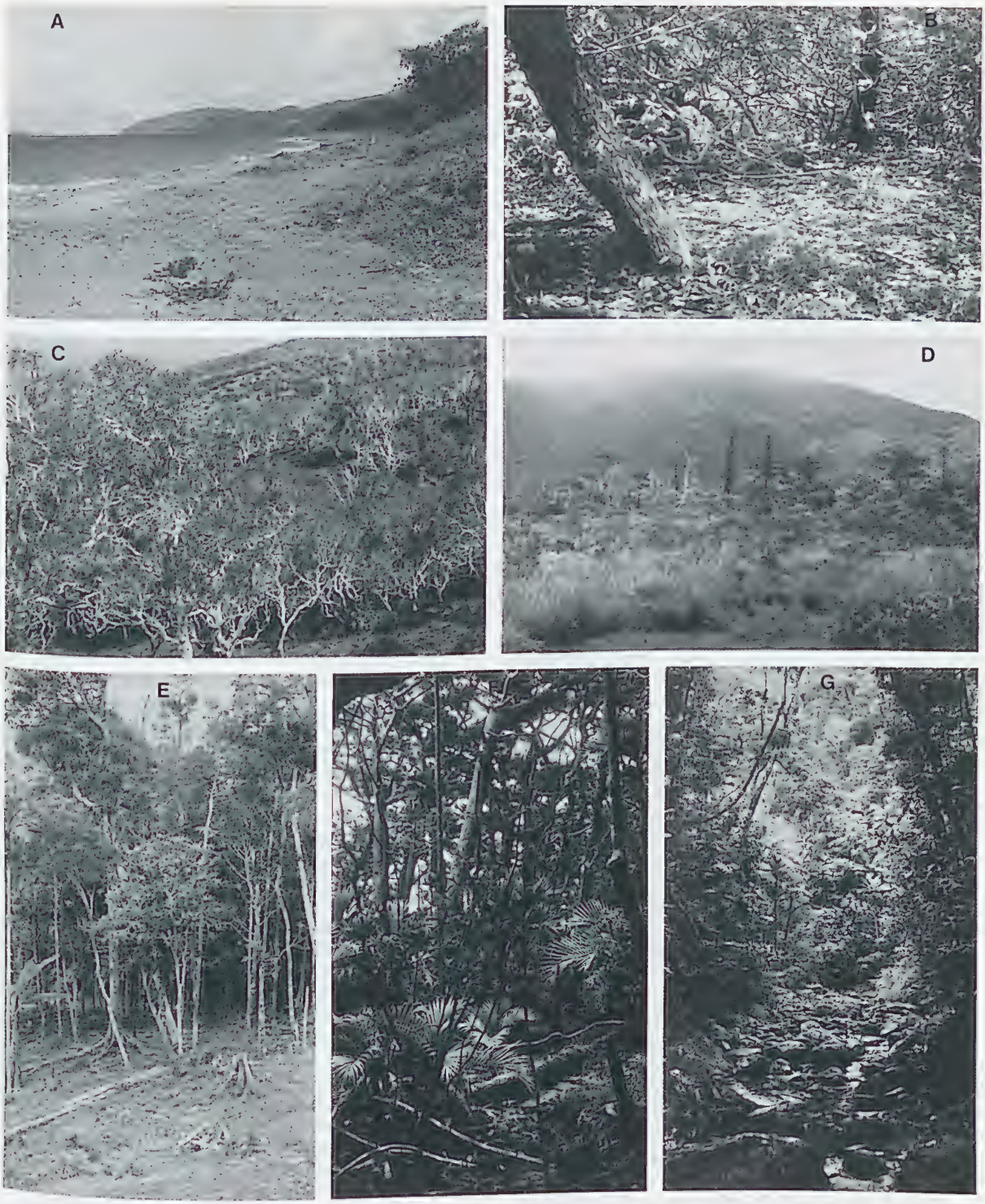


Fig. 1. Overview of some of the major habitats encountered on the New Caledonian mainland. **a,** Coastal landscape at Houaliou, typical of the mideastern and northern coastline of mainland New Caledonia. **b,** Coastal scrub backing beach front at Houaliou. **c,** Naueliu woodland on coastal hillslopes at Puebo. **d,** Heath and conifer scrub on the Plaine des Lacs. **e,** Lowland rainforest edge on coastal hillslope at Mt Dore, here bordered by a plantation clearing. **f,** Mountain stream passing through mid altitude rainforest (500 m) on Mt Aoupinie. **g,** Interior of mid to high altitude rainforest (900–1000 m) on Mt Panie.

Historical Resume

By 1900, Bavay (1869) and Bocage (1873b) had described nine of the currently recognized scincid lizards of New Caledonia, and Boulenger (1887) had collectively reviewed the described taxa while cataloguing specimens held in the British Museum. Aside from Roux's (1913) major review of the New Caledonian herpetofauna (which included several new taxa), subsequent taxonomic studies dealing with the scincid lizards of the island have generally been confined to describing new taxa as they became known. The taxonomic contributions of previous authors are given below in chronological order, and where appropriate comments on types are included.

Peters (1869) described *Lygosoma (Mocoa) nigrofasciolatum* from a single specimen, still in existence and lodged in the ZMB.

Bavay (1869) described eight new scincid lizard species. No types were listed and no indication given as to where the specimens on which the descriptions were based were lodged. For five of these taxa no types have been found and are here presumed lost (see species accounts for *P. garnieri, M. tricolor, L. nigrofasciolatum, C. austrocaledonicus* and *T. variabilis)*. Specimens on which three Bavay taxa were based are lodged in the BM. These are labelled as having been presented by Bavay and coming from New Caledonia and were listed as types by Boulenger (1887) (see species accounts for *S. deplanchei, N. mariei* and *N. gracilis)*.

Bocage (1873b) described three new lizard species from New Caledonia (see species accounts for *T. aubrianus, L. steindachneri* and *L. nigrofasciolatum)*. No formal types were designated for Bocage's species but the specimens upon which the descriptions were based were lodged in the Lisbon Museum. These syntypes were later examined by Roux (1913) and compared with the specimens collected by Roux & Sarasin from New Caledonia. These and other specimens in the collection of Bocage were lost when the Lisbon Museum was destroyed bt fire (18th March 1973).

Günther (1872) described four taxa from specimens purportedly obtained from the Feejee Islands' during the voyage of the *Curacoa* (see species accounts for *C. austrocaledonicus, S. deplanchei, N. mariei* and *N. gracilis)*. Specimens on which these descriptions were based are lodged in the BM, and were listed as types of Günther's species by Boulenger (1887). None of these taxa have since been recorded from the Fiji Islands. The *Curacoa* also visited New Caledonia during its voyage and this is considered the more likely place of origin for the specimens on which Günther's species are based.

Brocchi (1876) described the large and unique *Eumeces bocourti* from a single specimen, now lodged in the MNHP.

Peters (1879) described *Sauroscincus braconnieri* (= *Tropidoscincus aubrianus* Bocage) from a single subadult specimen in the ZMB.

Boulenger (1887) recognised only eight of the existing New Caledonian taxa, redescribing them from specimens in the BM (see species accounts for *L. nigrofasciolatum, M. tricolor, T. variabilis, C. austrocaledonicus, P. garnieri, S. deplanchei, N. mariei* and *N. gracilis). No mention was made by Boulenger of Tropidoscincus aubrianus* Bocage.

Andersson (1908) described *Lygosoma rohssii* from a series of 3 adults in the NHMG.

Werner (1909) described *Lygosoma euryotis* from a single specimen in the MRHN.

Roux (1913) reviewed the New Caledonian skinks and most of the existing taxa and synonyms previously recognized by Boulenger (1887) were redescribed. Of the taxa described since Boulenger's catalogue, Roux redescribed *Lygosoma euryotis* Werner from the type, and synonimized *Lygosoma rohssii* Andersson with *L. variabilis* Bavay. Several new taxa were described by Roux as subspecies of *Lygosoma austro-caledonicum,* the validity of which are discussed later. No types were designated by Roux for new taxa, but a list of localities for specimens collected by Roux & Sarasin was given. Roux did however list the types examined for a number of existing species, most importantly those of Bocage (1873b) with which Roux made direct comparisons to conspecific specimens in the collection of Roux & Sarasin.

Since Roux's revision few new taxa have been described. Parker (1926) described *Lygosoma (Leiolopisma) novaecaledoniae* from a single specimen in the BM; Mertens (1928) described *Cryptoblepharus boutonii novo-caledonicus* from specimens in the NHMB and SMF; Loveridge (1941) described *Lygosoma sleveni* from specimens in the MCZ (originally part of the Roux & Sarasin collection in the NHMB); Böhme described *Eugongylus haraldmeieri* (1976) and *Leiolopisma greeri* (1979) from recent collections made by Harold Meier; Kramer (1979) designated lectotypes for taxa described by Roux (1913) from the collections made by Roux & Sarasin and lodged in the NHMB: (see species accounts for *C. austrocaledonicus, C. atropunctatus* and *C. festivus)*.

Natural history notes on New Caledonian scincids were provided by Meier (1979a,b) and Mertens (1964).

Systematics

Greer (1974) considered the New Caledonian scincid fauna to belong to the *Eugongylus* group of the subfamily Lygosominae. In reviewing the generic relationships of *Leiolopisma* and its relatives, Greer (1974) diagnosed monophyletic lineages for a number of associated genera including the endemic New Caledonian genus *Phoboscincus* Greer and widespread *Cryptoblepharus* Weigmann which has a single representative in New Caledonia. The remaining New Caledonian species recognized by Greer were largely incorporated into *Leiolopisma* Duméril & Bibron and *Anotis* Bavay.

Leiolopisma as conceived by Greer at this time was a diverse assemblage of generally primitive species with a wide distribution incorporating Mauritius (Round Island), the eastern and southern Australian coasts, New Zealand, New Caledonia, and more recently Vanuatu and Fiji. The first step towards clarifying relationships between the species included in *Leiolopisma* (sensu Greer) was to define species groupings where possible. The following groupings are now recognised by me for the New Caledonian species fomerly assigned to *Leiolopisma,* and include several new and resurrected taxa: 1) *Lygosoma nigrofasciolatum* Peters and *Leiolopisma greeri* Böhme; 2) *Tropidolopisma variabilis* Bavay, *Tropidoscincus aubrianus* Bocage and *Lygosoma rohssii* Anderson; 3) *Lygosoma tricolor* Bavay and *Lygosoma euryotis* Werner; 4) *Lygosoma austro-caledonica* Bavay, *Lygosoma austro-caledonicum atropunctatum* Roux, *Lygosoma austro-caledonicum festivum* Roux and *Lygosoma orestes* n. sp.; 5) *Lygosoma deplanchei* Bavay is a monotypic group in the *Eugongylus* group, but further definition of relationships remains obsure. Members of groups 1–4 are diagnosed as each other's closest relatives by a suite of derived character states, but relationships between the groups are often unclear.

From these species groupings of New Caledonian *Leiolopisma* the following generic reallocations are here proposed: *Tropidoscincus* Bocage for group 2; *Marmorosphax* n. gen. for group 3; *Caledoniscincus* n. gen. for group 4; *Sigaloseps* n. gen. for group 5. The following species are retained in *Leiolopisma* pending a review of *Eugongylus* group systematics: *L. nigrofasciolatum, L. greeri, L. steindachneri, L. novaecaledoniae.*

Greer (1974) used *Anotis* (type species *Anotis mariei* Bavay, 1869) to encompass the Australian species *Saiphos maccoyi* Lucas & Frost and *Lygosoma graciloides* Lönnberg & Andersson, and the New Caledonian species *Anotis mariei* Bavay, *Lygosoma gracile* Bavay and *Lygosoma sleveni* Loveridge. For these same species the generic classification was later amended to *Nannoscincus* by Czechura (1981) on the basis of the observation by Cogger (1979) that *Anotis* was preoccupied. *Nannoscincus* is here restricted to the New Caledonian species and the Australian species *Saiphos maccoyi* Lucas & Frost. *Lygosoma graciloides* Lönnberg & Andersson is only distantly related to the group and awaits generic placement.

Materials and Methods

The generic classification presented here is based on diagnoses featuring single unique derived characters and/or unique combinations of shared derived character states, within the context of the phylogenetic subdivisions of the subfamily Lygosominae, as presented so far by Greer (1974, 1982).

Species accounts present synonomies of nomenclatural significance only and in most cases are based on examination of type material. Where appropriate, lectotypes have been designated from syntype series. Where types are no longer extant, neotypes have been designated. This has been extended to junior synonyms where confusion with superficially similar taxa may arise. Neotype designations were required for *Lygosoma arborum, Tropidolopisma variabilis, Lygosoma tricolor* and *Lygosoma austro-caledonica.* The specimens upon which Bavay (1869) based descriptions of these species are apparently lost. Similar designations were needed for the Bocage (1873b) New Caledonian scincid types *(Lygosoma deplanchei, Lioscincus steindachneri, Tropidoscincus aubrianus)* lost when the Lisbon Museum was destroyed. Descriptions, line drawings and photographs of type material have been presented where possible. A general description of each species shows variation in features of morphology.

Measurements are expressed as percentages of the snout to vent length (SVL).

Scalation: those characters regarded as necessary to identify the species from one another, or that are unusual and may be of interest when related to specialized habits of certain species, are discussed.

Head: terms used (Figs 2, 3) generally follow Taylor (1935: 11) except for the shields bordering the anterior and lower edge of the orbit which follow Sadlier (1984).

Body: 'midbody scale rows' are the number of longitudinal scale rows around the body counted at a point midway between the axilla and groin;

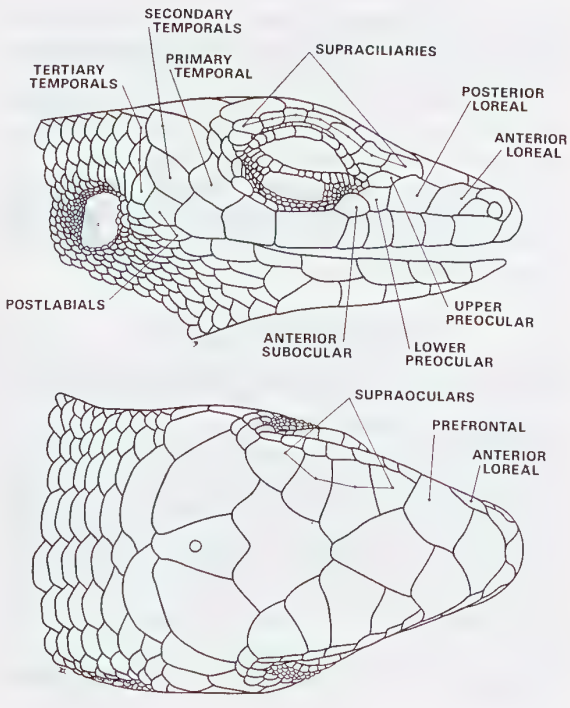


Fig. 2. Dorsal and lateral views of the head of ZMB 9702 (holotype of *Sauroscincus braconnieri* Peters), a specimen of *Tropidoscincus aubrianus* Bocage with some of the major headshields labelled.

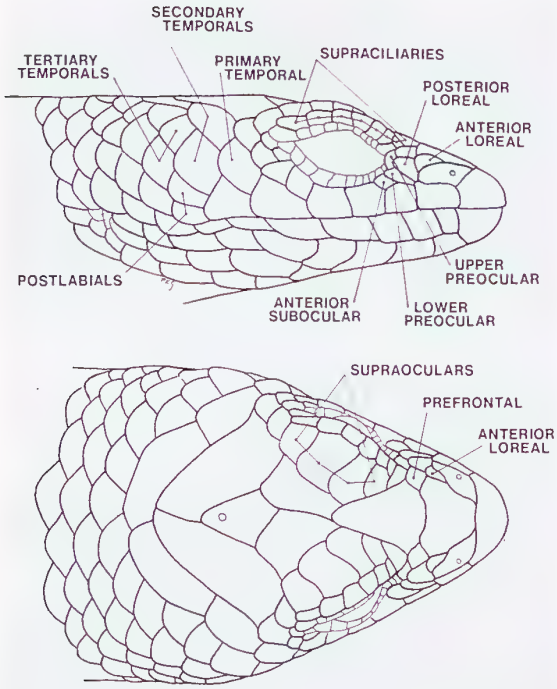


Fig. 3. Dorsal and lateral views of the head of NHMB 7232, a specimen of *Nannoscincus sleveni* with some of the headshield configurations peculiar to *Nannoscincus* labelled.

'paravertebral' scales are the number of scales in a paravertebral row posterior to the parietals to a point opposite the anus.

Grid coordinates for specimen localities have been obtained from the official Standard Names Gazateer for New Caledonia and Wallis and Futuna produced by the U.S. Board on Geographic Names (1974). Grid coordinates for localities were then compared with a 1/500000 Nouvelle Caledonie Map produced by Institut Géographique National, prior to plotting.

Geoscincus n. gen.

Type species. *Eugongylus haraldmeieri* Böhme, 1976: 248

Diagnosis. Supranasals absent; last upper labial greatly reduced and repositioned posteriorly; temporal and posterior head shields fragmented; parietals each bordered by 2 upper secondary temporals, single nuchal and internuchal; chinshields 2, second pair and post genials seperated from contact with lower labials by row of small lateral chin scales; auricular lobules absent; premaxilliary teeth 6–9; large size (maximum SVL 112 mm).

Recognized species. *Geoscincus haraldmeieri* (Böhme, 1976).

Etymology. The name *Geoscincus* combines the Greek for earth *(geo)* with Neo-Latin for skink *(scincus)*.

Remarks. Böhme (1976) thought *Eugongylus haraldmeirei* bridged the differences between *Eugongylus* Fitzinger, *Tachygia* Mittleman and *Phoboscincus* Greer and synonomized the latter two genera with *Eugongylus*.

The suite of characters diagnosing *Eugongylus haraldmeirei* Böhme is unique and does not allow ready placement in recognized groups within the lygosomines. On this basis, Böhme's concept of *Eugongylus* is here rejected, and *Eugongylus haraldmeirei* Böhme placed in the monotypic genus *Geoscincus*.

Geoscincus haraldmeieri (Böhme)

Figs 4–7

Eugongylus haraldmeirei Böhme, 1976: 248.

Type material. HOLOTYPE: *Eugongylus haraldmeirei* Böhme, ZFMK 15888, adult male, SVL 112 mm (Figs 4, 5), Coula, (500 m), New Caledonia, 21°21′S 165°27′E. PARATYPE: ZFMK 15889, same locality as holotype.

Diagnosis. Same as genus.

Description. MEASUREMENTS: snout to vent length 88–112 mm (paratype and holotype respectively); distance from axilla to groin 55.4–56.2% of SVL ($\bar{x}$ = 55.8, n = 2); distance from forelimb to snout 37.5–39.8% of SVL ($\bar{x}$ = 38.6, n = 2); hindlimb length 32% of SVL (n = 2).

SCALATION: frontonasal broader than long (W/L 130–150%, $\bar{x}$ = 140, n = 2); prefrontals large, narrowly separated; frontal longer than broad (W/L 69–71%, $\bar{x}$ = 70, n = 2); frontoparietals distinct; interparietal distinct; parietals each bordered by 2 upper secondary temporals, a single nuchal and an internuchal scale; scales of temporal region forming an irregular pattern posterior to last enlarged upper labial (1 of Fig. 6) and possibly best interpreted as primary temporals 2 (3a and 3b of Fig. 6), upper secondary temporals 2 (4a and 4b of Fig. 6), lower secondary temporal usually divided (5a and 5b respectively of Fig. 6) or fused to form a single scale (right side of holotype), tertiary temporals 3 (6a, 6b and 6c of Fig. 6), and postlabials 2 (7a and 7b of Fig. 6).

Nasals narrowly to moderately separated; 2 loreals in a horizontal sequence, anterior nearly as deep as long, posterior longer than deep; anterior subocular single; supraciliaries 7, sixth large and intruding between third and fourth supraoculars, first failing to contact frontal; enlarged upper labials usually 6 (7 right side of holotype) with fifth usually subocular and considerably deeper than long, last upper labial (2 of Fig. 6) apparently squeezed out of position by shortening of snout; lower labials 6–7, first 2 contacting postmental; chinshields 2, first pair in moderate contact, second pair variably separated from lower labials by a single row of small intervening scales.

Lower eyelid scaled, contacting subocular upper labial.

Ear opening with no enlarged auricular lobules.

Body scales small, smooth; midbody scale rows 46–48 ($\bar{x}$ = 47, sd = 1, n = 2) paravertebral scales 113–116

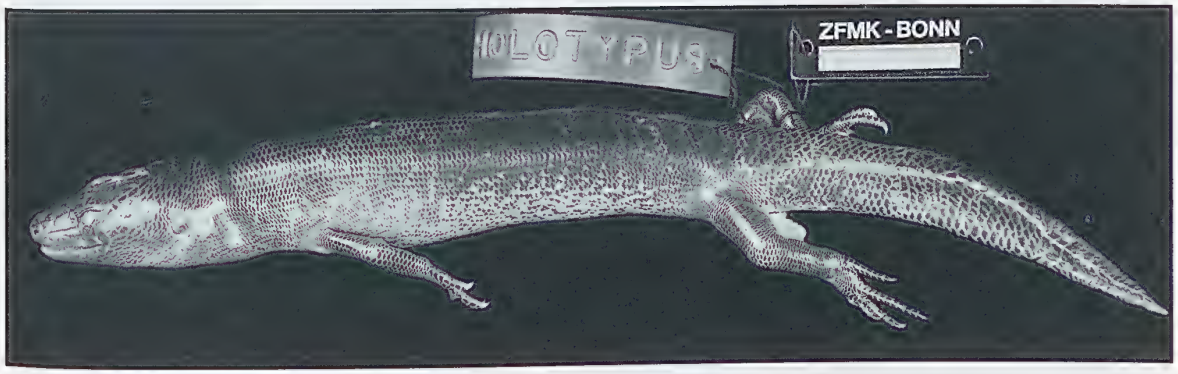


Fig. 4. ZFMK 15888, holotype of *Eugongylus haraldmeirei* Böhme.

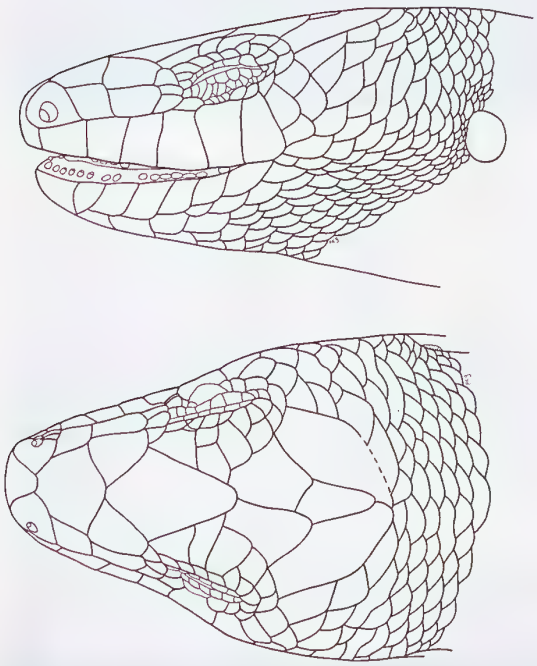


Fig. 5. Lateral and dorsal views of the head of ZFMK 15888, holotype of *Eugongylus haraldmeirei* Böhme.

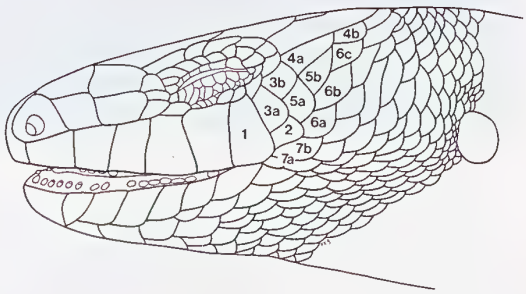


Fig. 6. Major lateral headshields in posterior region of head of *Geoscincus haraldmeirei* (ZFMK 15888) labelled as described in text. Normally two distinct upper labials occur posterior to subocular upper labial and scales that define free edge, upper and lower jaws meet at or slightly posterior to post labials. In *G. haraldmeieri* free edges of upper and lower jaws meet just past penultimate upper labial (part 1 of this figure).

($\bar{x} = 114.5$, sd = 1.5, n = 2).

Lamellae beneath fourth toe 19.

OSTEOLOGY: premaxillary teeth 6 or 9; presacral vertebrae 29; phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4, respectively.

COLOUR AND PATTERN: dorsal surface grey to brown, head similiar. Lateral surface grey with fine, sparse, white flecking most prominent lateroventrally and anteriorly. Limbs grey to brown above, becoming lighter beneath. Venter posterior of forelimbs grey-brown, anterior of forelimbs cream with a fine brown mottle (each scale in this region has a brown fleck).

Distribution and Habitats. Known only from the type locality, Coula (500 m asl), on mainland New Caledonia (Fig. 7). Both the holotype and paratype were found in a fallen decaying tree trunk in a well forested area.

Genus *Phoboscincus* Greer

Phoboscincus Greer, 1974: 15 (type species *Eumeces bocourti* Brocchi, 1876, by original designation).

Diagnosis. Large (maximum SVL 200–275 mm) skinks; frontoparietals fused; teeth in anterior part of both upper and lower jaws sharply pointed, recurved and fang-like.

Recognized species. *Phoboscincus bocourti* (Brocchi, 1876); *Phoboscincus garnieri* (Bavay, 1869).

Phoboscincus bocourti (Brocchi)

Figs 8–10

Eumeces bocourti Brocchi, 1876: 95.

Type material. HOLOTYPE: MNHP 3029, *Eumeces bocourti* Brocchi (Figs 8, 9, 10).

Fig. 7. Distribution of *Geoscincus haraldmeirei* (open star in closed circle), *Phoboscincus garnieri* (closed circle = specimen records, open circle = literature records) and *Graciliscincus* (closed square) in New Caledonia.

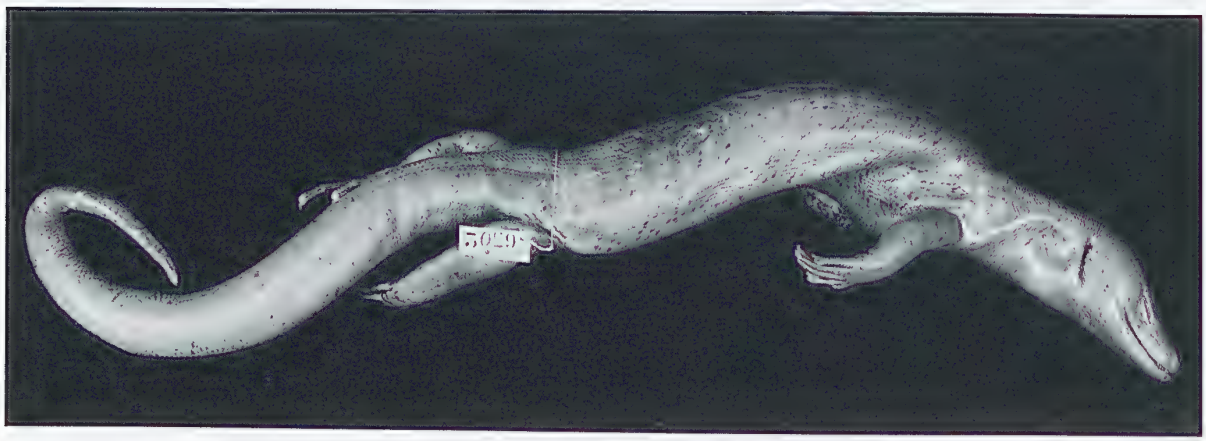


Fig. 8. MNHP 3029, holotype of *Eumeces bocourti* Brocchi.

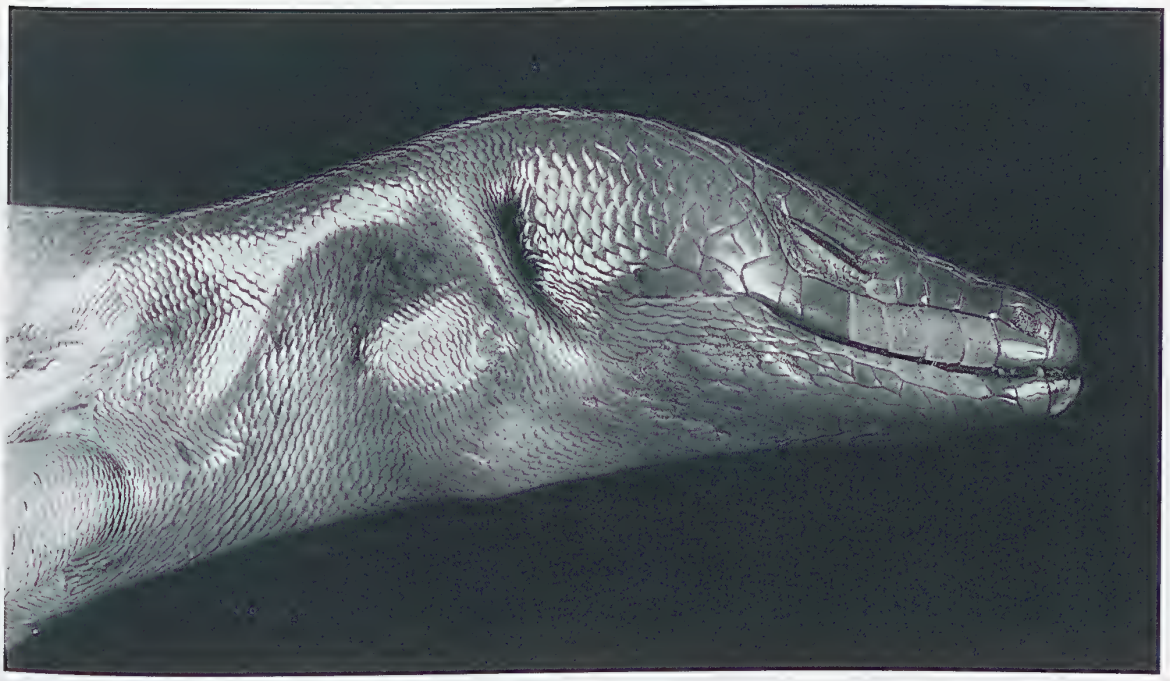


Fig. 9. Closeup of the lateral view the of head of MNHP 3029 holotype of *Eumeces bocourti* Brocchi, showing depressed snout and massive jaw musculature.

Diagnosis. *Phoboscincus bocourti* is distinguished from the only other species in the genus, *Phoboscincus garnieri,* by: larger size (maximum SVL ca. 275 mm vs SVL 200 mm); more numerous scales at midbody (ca. 66 vs 32–34); supranasals narrowly separated (vs broadly contacting); uniformly dark colouration (vs colour pattern of broad, dark bands on a light background).

Description. *Phoboscincus bocourti* is a large skink known only from a single specimen.

MEASUREMENTS: SVL ca. 275 mm, preserved in an undulating curve; distance from axilla to groin 165 mm = 60% of SVL; distance from forelimb to snout 102 mm = 37.1% of SVL; hindlimb length 93 mm = 33.8% of SVL; tail length 270 mm (reproduced).

SCALATION: supranasals narrowly separated; frontonasal wider than long (W/L 140%); prefrontals moderately separated, extending laterally to contact third upper labial; frontal as broad as long (W/L 111%); frontoparietals fused; interparietal distinct; parietals each bordered by 2 enlarged upper secondary temporals and a single nuchal only marginally larger than adjacent scales of nape; primary temporal and lower secondary temporal fragmented, appearing as numerous similarly sized scales.

Nasals widely separated; anterior loreal as deep as combined nasal and supranasal depth, excluded from contact with posterior loreal by venterolateral extension of prefrontal to contact third upper labial; posterior loreal as deep as anterior loreal (alternatively viewed as the third loreal in a horizontal sequence of which the second has been incorporated into prefrontal); anterior

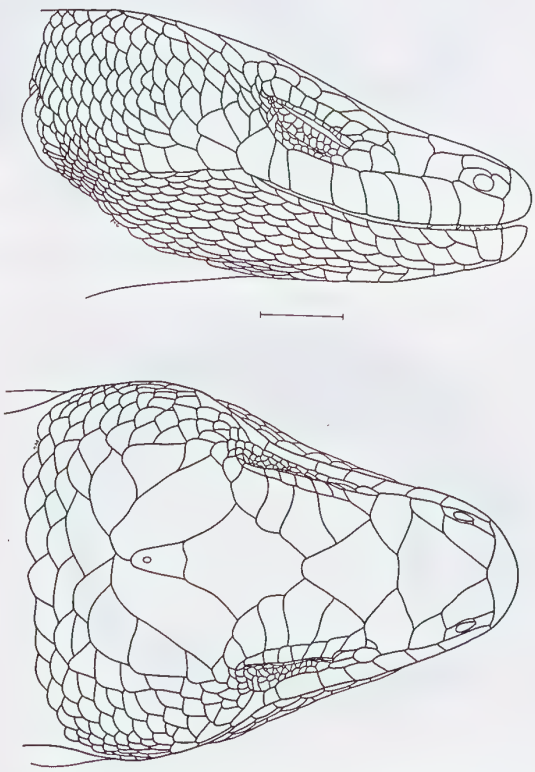


Fig. 10. Lateral and dorsal views of the head of MNHP 3029, holotype of *Eumeces bocourti* Brocchi.

subocular single, small, only marginally larger than surrounding scales of lower eyelid; supraciliaries 7; upper labials 8/9, last divided by a diagonal suture and penultimate on right divided to give an extra labial, sixth subocular both sides and contacting the lower eyelid; lower labials 9/10, first 2 contacting postmental; chinshields 3, first pair meeting medially, second and third pairs separated from labials by 1 or more intervening rows of smaller scales.

Lower eyelid scaled, contacting subocular upper labial.

Ear opening with 3 obtuse, enlarged auricular lobules anteriorly.

Body scales smooth, small; midbody scale rows ca. 66.

Lamellae beneath fourth toe 31/33.

OSTEOLOGY: presacral vertebrae 30; phalangeal formula for manus and pes 2.3.4.?.? and 2.3.4.5.4., respectively.

Distribution. New Caledonia.

Phoboscincus garnieri (Bavay)

Figs 7, 11–13

Eumeces garnieri Bavay, 1869: 15.

Type material. NEOTYPE: *Eumeces garnieri* Bavay, BM 1860.3.18.18, here designated, adult male, SVL ca. 200 mm (Figs 11, 13).

Additional material examined. NHMB 7136, Outbache, 20°26′S 164°38′E; NHMB 7137-38, Ngoi Tal, 21°49′S 166°36′E; NHMB 7139, Quenepee, Lifou, Loyalty Islands; BM 1926.9.17.61, 1926.9.17.16, New Caledonia.

Diagnosis. *Phoboscincus garnieri* is distinguished from the only other species in the genus, *Phoboscincus bocourti,* by: smaller size (maximum SVL 200 mm vs ca. 275 mm); fewer scales at midbody (32–34 vs ca. 66) supranasals broadly contacting (vs narrowly seperated); colour pattern featuring broad, dark transverse bands on a light background (vs uniformly dark).

Description. This description is based on seven adult specimens.

MEASUREMENTS: maximum SVL ca. 200 mm; distance from axilla to groin 54.5–55.2% of SVL

Fig. 11. BM 1860.3.18.18, neotype of *Eumeces garnieri* Bavay.

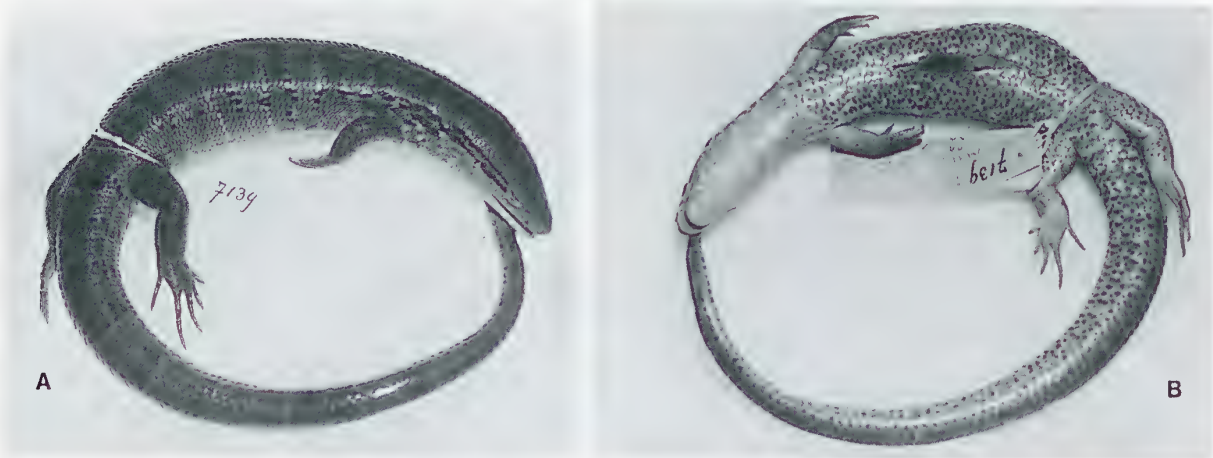


Fig. 12. NHMB 7139, a specimen of *Phoboscincus garnieri* (Bavay) showing the distinctive dorsal bands **(a)**, and dark ventral markings **(b)** of this species.

($\bar{x}$ = 54.9, n = 6); hindlimb length 35.9–42.2% of SVL ($\bar{x}$ = 38, n = 7); tail length 204% of SVL (n = 1).

SCALATION: supranasals in broad contact medially; frontonasal broader than long (W/L 117.3–154.8%, $\bar{x}$ = 129.6, n = 6); prefrontals large, moderately to widely separated; frontal longer than broad (W/L 77.8–90.9%, $\bar{x}$ = 84.2, n = 6); frontoparietals fused; interparietal distinct; parietals each bordered by a single nuchal and upper secondary temporal scale; primary temporals usually 2 (92.8%), rarely a single larger scale; upper secondary temporal single; scales of temporal region posterior to primary temporals and divided last upper labial fragmented.

Nasals widely separated; 2 loreals in a horizontal sequence, anterior as deep as nasal and supranasal combined, posterior broad as deep; anterior subocular single; supraciliaries 6(61.5%, n = 7)–7; upper labials 8 with sixth subocular and contacting lower eyelid; lower labials 6(70%, n = 5)–7, first 2 contacting postmental; chinshields 2, first pair moderately narrowly separated (71.4%, n = 6) or in point contact, all chinshields contacting lower labials but anterior half of post genial only contacting lower labials.

Lower eyelid scaly, central scales markedly larger than those at perimeter and resembling a large opaque disc divided by median sutures.

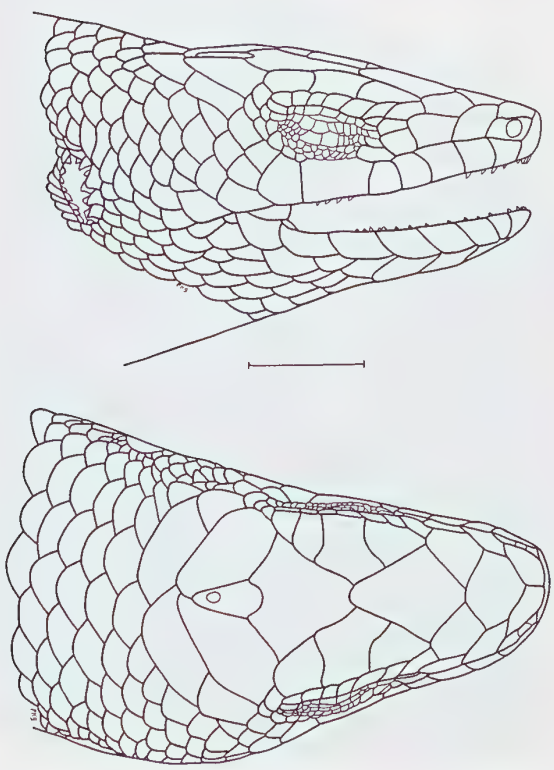


Fig. 13. Lateral and dorsal views of the head of BM 1860.3.18.18, neotype of *Eumeces garnieri* Bavay.

Ear opening with 1–4, usually 3 (92.8%, n = 7), acute auricular lobules anteriorly.

Body scales smooth to faintly striate; midbody scale rows 32–34 ($\bar{x}$ = 32.6, sd = 0.9, n = 7); paravertebral scales 74–83 ($\bar{x}$ = 79, sd = 2.6, n = 7).

Lamellae beneath fourth toe 23–27 ($\bar{x}$ = 24.2, sd = 1.2, n = 7).

OSTEOLOGY: premaxillary teeth 10(33%, n = 3)–11; maxillary teeth 21–25 ($\bar{x}$ = 23, sd = 1.5, n = 3); dentary teeth 24–30 ($\bar{x}$ = 28.5, sd = 2.3, n = 3); presacral vertebrae 29 (n = 6); phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4, respectively.

COLOUR AND PATTERN: dorsal surface grey with a series of broad brown bands, often extending laterally but becoming poorly defined. Black temporal streak of variable width extending from eye posteriorly along dorsolateral surface to just past forelimb, breaking into series of longitudinally aligned dark dashes along dorsum. Venter white with prominent dark flecking posterior to forelimb; throat and chin less intensely marked in specimens from Lifou and Ngoy Tal; sparse dark flecks over most of venter, throat and tail in specimen from Outbache.

Distribution and habitats. *Phoboscincus garnieri* is sporadically distributed on mainland New Caledonia and offshore islands (Fig. 7), and also occurs on Lifou and possibly Ouvea Islands in the Loyalty Islands group.

Neither Bavay or Roux (1913) give an account of the habits of this species. I observed a large lizard I believe to be *P. garnieri* at Koumac Caves in far north-west New Caledonia. The single individual was on a hillslope of scattered limestone boulders with moderately thick woodland. When disturbed it sought refuge beneath a rock outcrop, and later climbed a small tree.

Reproduction. Two females collected by Roux & Sarasin contained 5(2/3) and 8(4/4) enlarged, yolked ovarian follicles.

Remarks. Bavay (1869) described *Eumeces garnieri* from material from the island of "Ouen" off the southern coast of New Caledonia, (approximately 22°25′S 166°49′E). Only one set of measurements are in the original description and Bavay makes no mention of other specimens, apart from the observation of a large skink at Mouli on Ouvea Island in the Loyalty Islands group.

The description of Bavay and redescription by Boulenger (1887) of this species are in close agreement, differing only in the condition of the lower eyelid. Bavay describes "a transparent lower eyelid showing a disc not covered but surrounded by small scales", while Boulenger clearly describes the lower eyelid as scaly. BM 1860.3.18.18 almost certainly provided the basis for Boulenger's description and clearly has the lower eyelid scaled. The only discrepancy between this specimen and Boulengers redescription being length of the tail (an incomplete tail 300 mm long in description, while BM 1860.3.18.18 has an incomplete tail only 220 mm long).

In describing *Lygosoma garnieri* (Bavay) Boulenger (1887) incorrectly placed *Eumeces bocourti* Brocchi in

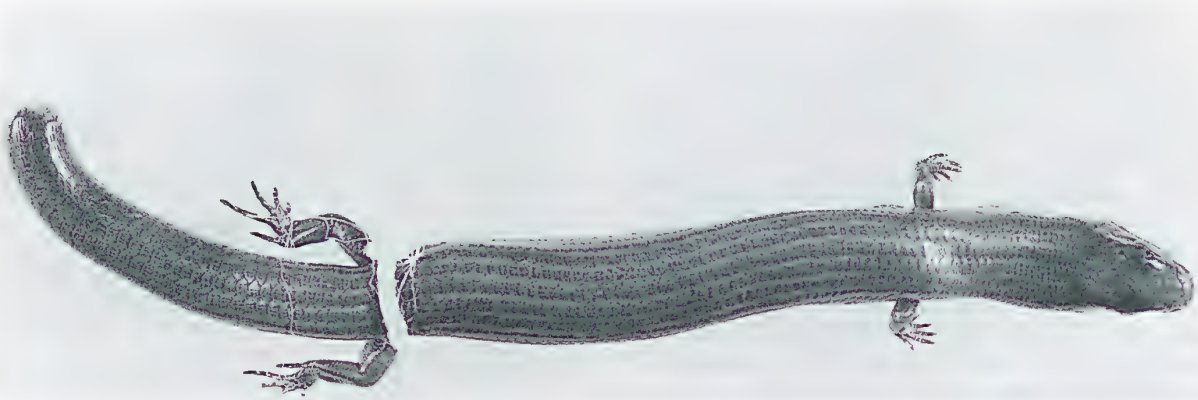


Fig. 14. AM R78143, holotype of *Graciliscincus shonae* n. gen., n. sp.

its synonomy. Roux (1913) later recognized *E. bocourti* Brocchi as distinct.

Graciliscincus n. gen.

Type species. *Graciliscincus shonae* n.sp., designated hereby.

Diagnosis. *Graciliscincus* can be distinguished from other genera in the *Eugongylus* group by the following combination of characters: depressed and elongate body form; supranasals absent; prefrontals small and widely separated; upper labials 5, third subocular; postmental contacting first lower labial only; lower eyelid with semi-transparent disc; ear opening minute; presacral vertebrae 36.

Etymology. The name *Graciliscincus* is derived from the Latin *gracilis* and *scincus*.

Remarks. Loss of phalanges on the digits of limbs and increase in postsacral vertebrae number are features often associated with a burrowing, semi-fossorial habit in skinks and have evolved independently in the *Sphenomorphus, Eugongylus* and *Egernia* groups in the Pacific region. *Graciliscincus shonae* is readily diagnosed as a member of the *Eugongylus* group of the scincid subfamily Lygosominae (Greer, 1979). It is unusual within the *Eugongylus* group in combining a high number of presacral vertebral (36) with a primitive phalangeal formula.

Graciliscincus shonae n. sp.

Figs 7, 14–16

Type material. HOLOTYPE: AM R78143, male, 4 km along the Mt Gouemba road from turnoff 3 km south of La Fause Yate Bridge, New Caledonia, 22°09′S 166°54′E, collected by R. Sadlier & P. Rankin, 27 Dec 1978 (Figs 14, 15). PARATYPE: CAS 159576, Mt Koghis (ca. 600 m) collected by A. Bauer, 28 Dec 1985.

Etymology. The species is named for Shona Sadlier.

Diagnosis. Species diagnosis same as for genus.

Description. Body form elongate with limbs and digits small, original part of tail stout. Known only from the types.

MEASUREMENTS: snout to vent length 37.5(holotype)–42(paratype) mm; distance from axilla to groin 64–65.5% of SVL ($\bar{x} = 64.7$, n = 2); distance from forelimb to snout 32–33.3% of SVL $\bar{x} = 32.6$, n = 2); hindlimb length 20–25% of SVL ($\bar{x} = 22.5$, n = 2); tail length 125% of SVL for regenerated tail of paratype.

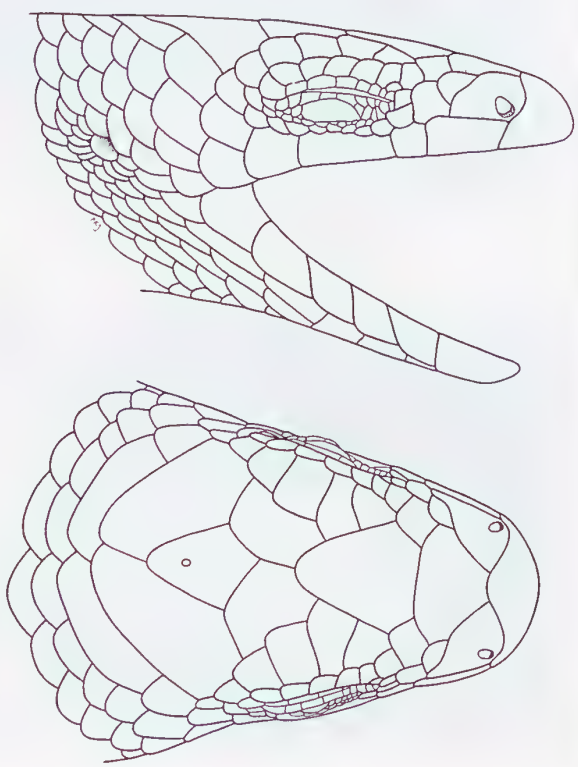


Fig. 15. Lateral and dorsal views of the head of AM R78143, holotype of *Graciliscincus shonae* n. gen., n. sp.

SCALATION: frontonasal nearly twice as broad as long (W/L 187.5–190.5%, $\bar{x}$ = 189, n = 2) prefrontals small and widely separated; frontal near or as broad as long (W/L = 90–100%, $\bar{x}$ = 95%, n = 2); frontoparietals distinct; interparietal distinct; parietals each bordered by a single nuchal and upper secondary temporal scale; primary temporal single; upper and lower secondary temporals each single; tertiary temporals 2.

Nasals large and moderately separated; anterior loreal semilunar, positioned on posterodorsal margin of nasal and failing to contact upper labials; posterior loreal as broad as deep, contacting nasal anteriorly; anterior suboculars 2; supraciliaries 6; upper labials 5, variable in length, first and third twice as wide as second, third subocular and contacting lower eyelid; postlabials 2; lower labials 5, postmental contacting first lower labial only; chinshields 2, first pair in broad contact.

Lower eyelid with an obvious, centrally located semi-transparent disc, length 50% of total eye length.

Ear opening small, circular and lacking enlarged auricular lobules.

Fig. 16. Mid altitude rainforest (300 m) beside road on low saddle on Mt Gouemba, type locality for *Graciliscincus shonae*.

Body scales smooth, scales of tail with 3 strong striations; midbody scale rows 22; paravertebral scales 76–80 ($\bar{x}$ = 78, sd = 2, n = 2).

Lamellae beneath fourth toe flattish and poorly differentiated from one another.

OSTEOLOGY: premaxillary teeth 13; maxillary teeth 23–24 ($\bar{x}$ = 23.5, sd = 0.5, n = 2); dentary teeth 28–29 ($\bar{x}$ = 28.5, sd = 0.5, n = 2); presacral vertebrae 36; phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4, respectively.

COLOUR AND PATTERN: dorsal surface midbrown with fine, dark longitudinal stripes extending from nape to tail tip (stripes consist of darker central section of each scale flanked by lighter brown); head dark brown with greyish tinge to supraocular, upper labial, rostral and nasal scales. Lateral surface similar to dorsal but lighter overall; no distinct demarcation of dorsal and lateral surfaces. Venter pale, each scale with fine brown spotting medially, more intense on lower labials to appear grey-brown.

Distribution and habitats. The only records for this species are from single specimens on either side of the southern part of the mainland (Fig. 7).

The specimen from Mt Gouemba was collected during cool weather from a patch of rainforest in a gully ca. 300–350 m (Fig. 16). It was under a small stone on the forest floor.

Genus *Leiolopisma* Duméril & Bibron

Leiolopisma Duméril & Bibron, 1839: 742 (type species *Scincus telfairi* Desjardin, 1831).
Eulepis Fitzinger, 1843: 22 (type species *Lygosoma duperreyi* Duméril & Bibron, 1839.
Cyclodina Girard, 1857: 195 (type species *Cyclodina aenea* Girard, 1857).
Hombronia Girard, 1857: 196 (type species *Hombronia fasciolaris* Girard, 1857).
Oligosoma Girard 1857: 196 (type species *Lygosomella aestuosa* Girard, 1857 = *Leiolopisma smithi).*
Lioscincus Bocage, 1873b: 228 (type species *Lioscincus steindachneri* Bocage, 1873).

Diagnosis. *Leiolopisma* is more an assemblage of generally primitive *Eugongylus* group species rather than a defineable group of related species. The species here included in *Leiolopisma* all lack distinct supranasal scales. This is the single derived character state for the genus.

Recognized species. The genus contains 39 known species: *L. telfairi* from Mauritius; 13 Australian species (see Cogger, 1986); 20 New Zealand species (see Gill, 1986); a single Fijian species (Zug, 1985); and four New Caledonian species. The four New Caledonian species are: *Leiolopisma nigrofasciolatum* (Peters), *Leiolopisma greeri* Böhme, *Leiolopisma steindachneri* (Bocage) and *Leiolopisma novaecaledoniae* (Parker).

Remarks. *Lygosoma nigrofasciolatum* Peters and *Leiolopisma greeri* Böhme are diagnosed as each other's nearest relatives by sharing a suite of derived character states, the distribution of which among other generally

primitive species in the *Eugongylus* group has yet to be determined. For this reason, these two species are retained in *Leiolopisma*. Similiarly, *Lioscincus steindachneri* Bocage and *Lygosoma novaecaledoniae* Parker, two generally primitive species with no obvious affinities to other species in the *Eugongylus* group of Greer (1974), are retained in *Leiolopisma*. While realizing the artificial nature of grouping these New Caledonian species into *Leiolopisma,* it is a matter of necessity to provide these species with some generic allocation. *Leiolopisma* at this time best serves this purpose. Should *Eulepis* Fitzinger, 1843, and *Cyclodina* Girard, 1857, be diagnosed and recognized as monophyletic lineages, so too should *Leiolopisma* Duméril & Bibron, 1839, be recognized as a monotypic genus restricted to its sole living representative *L. telfairi* Desjardin. *Oligosoma* Girard, 1857, would then be the available generic name for the residue of generally primitive skinks with a moveable lower eyelid containing a semi-transparent disc, and lacking supranasals.

Leiolopisma nigrofasciolatum species group

Diagnosis. Body scales smooth; last upper labial divided by an oblique suture; posterior chinshields separated from contact with labials by 1–2 rows of smaller intervening scales.

Recognised species. *Leiolopisma nigrofasciolatum* (Peters, 1869), *Leiolopisma greeri* Böhme, 1979.

Leiolopisma nigrofasciolatum (Peters).

Figs 17–22

Lygosoma (Mocoa) nigrofasciolatum Peters, 1869: 435.
Lygosoma arborum Bavay, 1869: 19.
Lygosoma deplanchei Bocage, 1873b: 229.

Type material. HOLOTYPE: *Lygosoma nigrofasciolatum* Peters, single specimen ZMB 6444, adult male, SVL 98 mm (Figs 18, 19), New Caledonia. NEOTYPES: *Lygosoma arborum* Bavay, AM R78029, here designated, adult male, SVL 100 mm (Fig. 20), Mouac Island off Poum, New Caledonia, 20°13′S 164°00′E. *Lygosoma deplanchei* Bocage, NHMB 7168, here designated, adult female, SVL 92 mm (Fig. 21), Outbache, New Caledonia, 20°26′S 164°38′E.

Additional material examined. AM R78027, 78028, Mouac Island off Poum, 20°13′S 164°00′E; AM R77969-70, Poum, 20°14′S 164°02′E; ABO, 20°17′S 164°26′E; NHMB 7161-62, 7164-66, 7169-70, Outbache, 20°26′S 164°38′E; AM R78050, Koumac Caves ca. 9 km east Koumac, 20°33′S 164°21′E; NHMB 7178, Toa, 20°33′S 164°48′E; NHMB 7163, Heinghene, 20°41′S 164°56′E; NHMB 7171-72, Kone, 21°04′S 164°52′E; AM R77686, 2 km north-east of Mt Aoupinie forestry camp by road (500 m), 21°08′S 165°21′E; AM R77602-05, Houailou airstrip, 21°16′S 165°37′E; NHMB 7177, Ni, 21°26′S 165°29′E; NHMB 7174-75, Canala, 21°32′S 165°57′E; AM R78249, 78282, 2 km west of Plum turnoff on Mt Dore road, 22°17′S 166°37′E; NHMB 7179, Brinor; NHMB 7180-1 Corala-Boreare.

Diagnosis. *Leiolopisma nigrofasciolatum* is distinguished from the only other species in the species group, *Leiolopisma greeri,* by: more paravertebral scales (82–96 vs 74); more lamellae beneath the fourth toe (28–34 vs 24–27); prefrontals moderately separated–point contact vs contacting narrowly.

Description. This description is based on four juvenile-subadults and 28 adult specimens (holotype and two hatchlings are not included in the analysis of measurements and scalation).

MEASUREMENTS: from our collection of this species made in December 1978, the smallest apparently reproductivly viable individuals were two females 73 and 77 mm SVL. From this data, juvenile-subadult (33–67 mm) and adult (73–108 mm) size classes are defined.

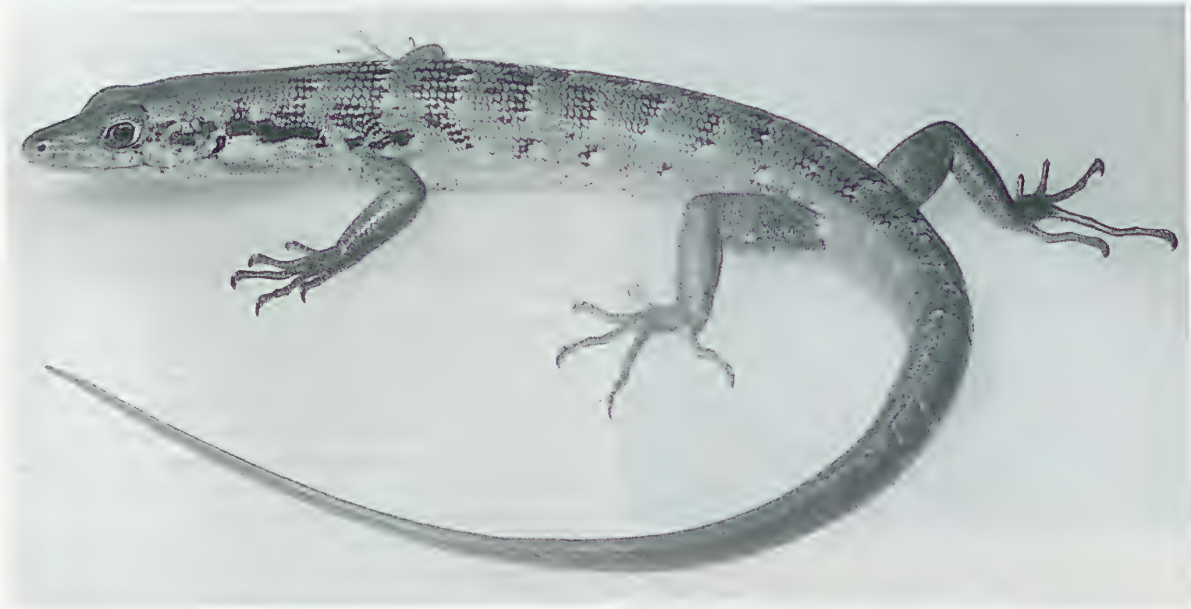


Fig. 17. *Leiolopisma nigrofasciolatum* (Peters) from Houailou airstrip, New Caledonia.

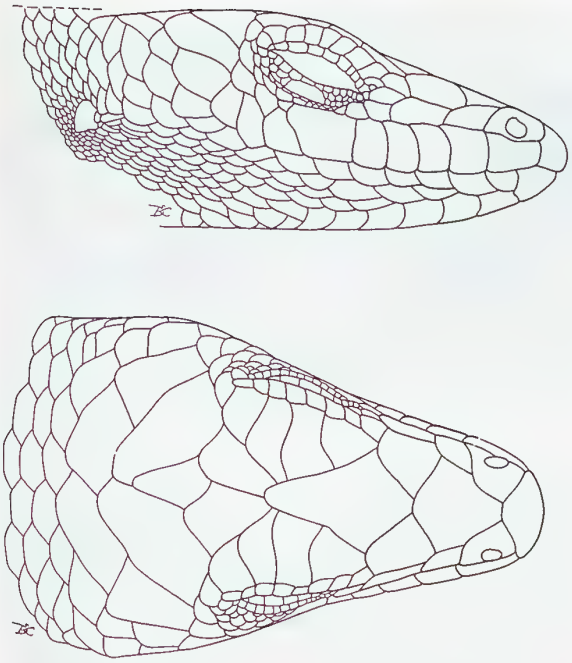


Fig. 18. Lateral and dorsal views of the head of ZMB 6444, holotype of *Lygosoma nigrofasciolatum* Peters.

Only adults are included in the following body measurements.

Maximum SVL 108 mm; distance from axilla to groin 50–60.7% of SVL ($\bar{x} = 55.6$, n = 28); hindlimb length 37–48.9% of SVL ($\bar{x} = 42.4$, n = 27); tail length ca. 146.3–179.1% of SVL ($\bar{x} = 162.6$, n = 13).

SCALATION: frontonasal as broad or broader than long (W/L 100–122%, $\bar{x} = 112$, n = 30); prefrontals large, usually moderately-narrowly separated (84.4%, n = 30) occasionally in point contact; frontal longer than broad (W/L 59–81%, $\bar{x} = 68\%$, n = 30); frontoparietals distinct; interparietal distinct; parietals each bordered by a single nuchal and upper secondary temporal scale; primary temporals 2 (though division of penultimate upper labial may give appearance of third primary temporal); upper and lower secondary temporals single, though division of last upper labial may give appearance of second lower secondary temporal; tertiary temporals 2, occasionally fused to give a single deep, slender scale (20%).

Nasals narrowly to moderately separated, occasionally with a crease from top of naris posteroventrally towards nasoloreal suture (crease sometimes appearing as a definite postnasal suture accompanied by considerable fragmentation of posterodorsal part of nasal scale; 2 loreals in a horizontal sequence, anterior twice as long as deep, posterior more than twice as long as deep and equal in depth to anterior loreal; anterior suboculars 1–2, second

Fig. 19. ZMB 6444, holotype of *Lygosoma nigrofasciolatum* Peters.

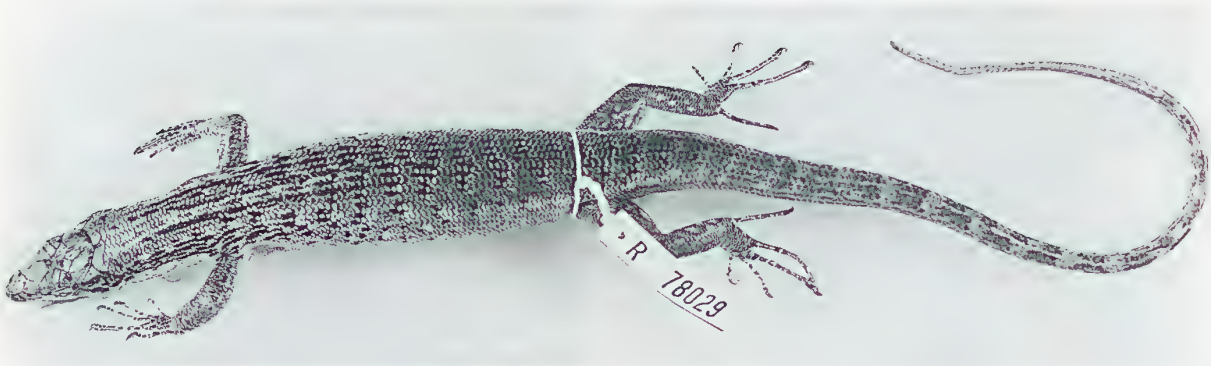


Fig. 20. AM R78029, neotype of *Lygosoma arborum* Bavay.

if present usually considerably smaller; supraciliaries usually 8 (91%, n = 32) rarely 7, 9 or 10; upper labials 8(48.4%, n = 31)–9 with sixth or seventh respectively subocular and contacting lower eyelid; penultimate upper labial often (53.6%, n = 14) divided by an oblique suture, last upper labial divided by an oblique suture, sometimes further fragmented to give 3 or 4 similar sized scales; postlabials usually 2 (63.3%, n = 30), each moderately deep and slender but often (26.7%) with lower subdivided by an oblique suture and occassionally (10%) fragmented so as to be indistinguishable; lower labials usually 7(56.2%, n = 32)–8(39%), rarely 6 or 9, first 2 usually contacting postmental; chinshields 4–5, first pair in broad contact and second pair usually in moderate contact, first pair also usually in partial contact with lower labials but all posterior chinshields separated from lower labials by 1–2 rows of smaller scales.

Lower eyelid with an obvious, centrally located semi-transparent disc, length 30–44% of total eye length ($\bar{x}$ = 36.7, n = 31).

Ear opening with 2–3 enlarged obtuse lobules anteriorly, uppermost largest, and numerous small rounded lobules on upper, lower and posterior edges.

Body scales smooth; midbody scale rows 36–42 ($\bar{x}$ = 38.2, sd = 1.4, n = 32); paravertebral scales 82–96 ($\bar{x}$ = 89, sd = 3.9, n = 32).

Lamellae beneath fourth toe 28–34 ($\bar{x}$ = 30.8, sd = 1.6, n = 30).

OSTEOLOGY: premaxillary teeth 11(66.6%, n = 12)–10; maxillary teeth 17–20 ($\bar{x}$ = 17.8, sd = 0.8, n = 12); dentary teeth 21–25 ($\bar{x}$ = 23.3, sd = 1.1, n = 11); presacral vertebrae 29 (n = 8); phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4, respectively.

COLOUR AND PATTERN: dorsal surface midbrown with greyish tinge and indistinct light and dark flecks randomly distributed anteriorly, but with dark flecks forming roughly transversely aligned bars posteriorly; dark longitudinal bar on nape in most individuals, sometimes extending to middorsum; head coppery brown, usually without light and dark flecking, dark edging may occur along scale sutures of most major head shields, lower labials with or without dark spotting. Dorsolateral surface with broad, dark streak extending from eye posteriorly over ear and continuing a variable distance towards forelimb, sometimes incorporating light flecks resulting in loss of continuity of dark band. Lateral surface similar to dorsal, but usually without dark transverse bars, and tending to become paler ventrally. Fore and hindlimbs similar to dorsum, either uniform brown or with varying degrees of light and dark markings. Venter immaculate, in life lime green as is underside of tail, limbs and soles of feet.

Some individuals nearly patternless, more or less

Fig. 21. NHMB 7168, neotype of *Lygosoma deplanchei* Bocage.

uniform midbrown above with occasional light or dark markings about forelimb.

Distribution and habitats. *Leiolopisma nigrofasciolatum* occurs over most of mainland New Caledonia on the coast, highlands (500+ m on Mt Aoupinie), and offshore islands (Isle Mouac off Poum) (Fig. 22). Roux (1913) also records this species from all three of Loyalty Islands.

Leiolopisma nigrofasciolatum is aboreal in habit and is usually encountered in open habitat such as low coastal scrub (Fig. 1a, b) and the edges of forest clearings at all altitudes. However, two specimens were taken from rock crevices in moderately tall but open woodland just north of Puebo (Fig. 1c), on the north-east coast.

Reproduction. *Leiolopisma nigrofasciolatum* is oviparous. One adult female (94 mm SVL) contained a total of seven shelled oviducal eggs (4/3). Two eggs from a clutch laid by a captive held specimen hatched in late February 1979. The young measured 34 and 33 mm SVL with bodyweights of 0.54 and 0.55 grams, respectively.

Remarks. The type of *Lygosoma (Mocoa) nigrofasciolatum* (ZMB 6444) agrees reasonably well with Peter's (1869) description and confirms the presence of distinct frontoparietals, a feature of scalation which readily distinguishes this species from the superficially similar *Emoia samoense* of nearby Pacific islands. The descriptions of *Lygosoma arborum* Bavay and *Lygosoma deplanchei* Bocage are sufficient to indicate these species are conspecific with *Lygosoma (Mocoa) nigrofasciolatum* Peters, but neotypes have been designated (above) to stabilize the names.

Leiolopisma greeri Böhme

Figs 22–24

Leiolopisma greeri Böhme, 1979: 140.

Type material. HOLOTYPE: *Leiolopisma greeri* Böhme, ZFMK 25456, adult female, SVL 61 mm (Figs 23, 24),

Fig. 22. Distribution of *Leiolopisma nigrofasciolatum* (closed circle) and *Leiolopisma greeri* (open star) in New Caledonia.

Koumac, New Caledonia, 20°34°S 164°17′E.

Diagnosis. *Leiolopisma greeri* can be distinguished from the only other species in the *Leiolopisma nigrofasciolatum* species group, *Leiolopisma nigrofasciolatum,* by: fewer paravertebral scales (74 vs 82–96); fewer lamellae beneath the fourth toe (24–27 vs 28–34); prefrontals contacting narrowly vs moderately separated–point contact.

Description. This description is based on the holotype ZFMK 25456.

MEASUREMENTS: SVL 61 mm; distance from axilla to groin 52.4% of SVL; hindlimb length 43.4% of SVL; tail length 120.5% of SVL, (regenerated).

SCALATION: frontonasal broad as long posteriorly (W/L 100%), considerably narrower anteriorly; prefrontals large, in narrow contact; frontal longer than broad (W/L 67%); frontoparietals distinct; interparietal distinct; parietals each bordered by a single nuchal and upper secondary temporal scale; primary temporals 2–3; upper and lower secondary temporals single; tertiary temporals fragmented, not readily discernable.

Nasals narrowly separated; 2 loreals in a horizontal sequence, posterior more elongate and less deep than anterior; anterior subocular single; supraciliaries 7/7; upper labials 8/8, with sixth subocular and contacting lower eyelid, last upper labial divided (giving appearance of an extra lower secondary temporal); postlabials indistinguishable; lower labials 7/6, first 2 contacting postmental; chinshields 4/3, those posterior to first pair partially to wholly separated from contact with lower labials by 1–2 rows of small scales.

Lower eyelid with an obvious, centrally located semi-transparent disc, length approximately 40% of total eye length.

Ear opening with 1–2 enlarged, white auricular lobules anteriorly, uppermost large and obtuse.

Body scales smooth; midbody scale rows 34; paravertebral scales 74.

Lamellae beneath fourth toe 24–27.

OSTEOLOGY: presacral vertebrae 29; phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4, respectively.

Fig. 23. ZFMK 25456, holotype of *Leiolopisma greeri* Böhme.

COLOUR AND PATTERN (in alcohol): dorsal and lateral surfaces with a pattern of thin, alternate black and cream transverse bars. Broad, pale midlateral stripe extending from upper labials through ear and over forelimb to groin. Tail mottled black and cream. Lower lateral surface mottled black and cream with dark spotting predominate and appearing as a continuation of dorsal and upper lateral colour. Venter immaculate white.

Distribution and habitats. *Leiolopisma greeri* is known only from the region of Koumac (20°34′S 164°17′E), in the north-west of mainland New Caledonia (Fig. 22). The type was collected from a "freshly fallen tree in montane forest" (Böhme, 1979).

Reproduction. *Leiolopisma greeri* is oviparous. Meier (1979a) records the type laying two eggs (7 x 3 mm) in January 1979. Size of young at birth was 30 mm SVL.

Remarks. *Leiolopisma greeri* first appeared (unnamed) in an article by Meier (1979a) who discussed the habits of this undescribed species in the field and in captivity.

Böhme (1979), in describing *Leiolopisma greeri,* draws attention to the problem of determining relationships within *Leiolopisma.* He refers to convergence in features of overall morphology between *Marmorosphax tricolor* and certain *Sphenomorphus* groups members, and between members of *Tropidoscincus* and the *Leiolopisma nigrofasciolatum*

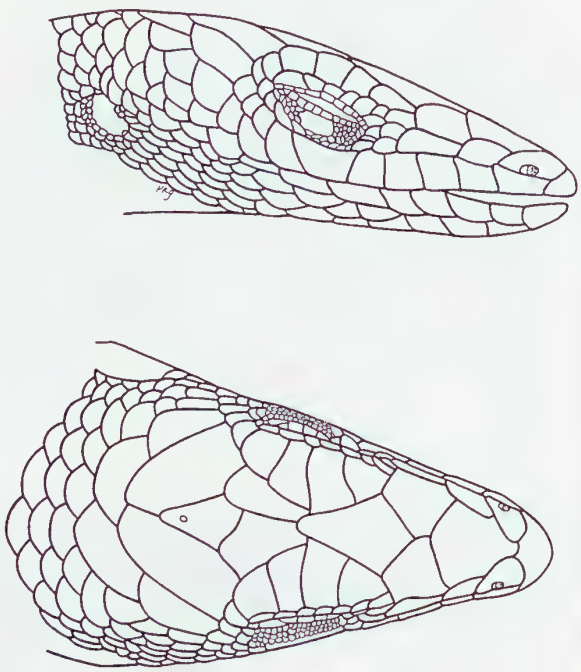


Fig. 24. Lateral and dorsal views of the head of ZFMK 25456, holotype of *Leiolopisma greeri* Böhme.

species group with certain species of *Emoia*. While Böhme regards *L. greeri* as "corresponding to the ecomorphtype of *L. nigrofasciolatum* and *L. variabile*" and that of "its close intrageneric relationships nothing can yet be said", I believe the suite of derived character states in the diagnosis for members of the *L. nigrosfasciolatum* species group serves to establish *L. nigrofasciolatum* and *L. greeri* as sister species.

Leiolopisma steindachneri (Bocage)

Figs 25–27, 29

Lioscincus steindachneri Bocage 1873b: 228.

Type material. NEOTYPE: *Lioscincus steindachneri* Bocage, NHMB 7450, here designated, adult female, SVL 87.5 mm (Figs 26, 27), from Mt Panie (500 m), New Caledonia, 20°36′S 164°46′E.

Additional material examined. NHMB 7470, Porari–Balade (200 m), 20°21′S 164°21′E; NHMB 7449, 7454-65, Mt Ignami (700 m), 20°28′S 164°36′E; NHMB 7466-69, Mt Panie (500 m), 20°36′S 164°46′E; AM R77723-28, 77800, creek crossing 1 km north-east of Mt Aoupinie forestry camp by road (500 m), 21°08′S 165°21′E.

Diagnosis. *Leiolopisma steindachneri* can be distinguished from all other New Caledonian members of the genus by the following combination of characters: frontoparietals fused; supranasals and post nasal suture generally absent; anterior loreal a small semilunar scale separated from contact with labials; ear lobules very small, barely distinguishable from surrounding small, blunt concial scales of upper, lower and posterior edges of ear opening; dorsal scales smooth.

Description. The basis of this description are 6 juvenile-subadult and 7 adult specimens.

MEASUREMENTS: the specimens we collected in December 1978 were assignable to juvenile (39–45 mm SVL) and adult (77–88.5 mm SVL) size classes, those collected by Roux & Sarasin in June and July 1911 to juvenile (35–45 mm SVL) and subadult (50.5–56 mm SVL) size classes, and two large adults of 86 and 102 mm SVL. Unless otherwise stated, only adults are included in the following body measurements.

Maximum SVL 102 mm; distance from axilla to groin 52.6–59.9% of SVL ($\bar{x} = 56.3$, $n = 7$); hindlimb length 42.9–49.4% of SVL ($\bar{x} = 45.9$, $n = 7$); tail length of 2 subadults 172–178.6% of SVL, ($\bar{x} = 174.7$, $n = 2$).

SCALATION: frontonasal usually slightly wider than long (W/L 94.3–137.5%, $\bar{x} = 111.5$, $n = 13$); prefrontals large, narrowly to moderately separated; frontal longer than broad (W/L 61.5–69.3%, $\bar{x} = 65.4$, $n = 13$); supraocular scales irregularly fragmented in certain individuals; frontoparietals fused, some individuals with a short median suture posteriorly; interparietal distinct; parietals each bordered by a fragmented nuchal and upper secondary temporal scale; nuchals divided to give up to 4 distinct scales, not noticeably larger than adjacent dorsals, bordering parietals between upper

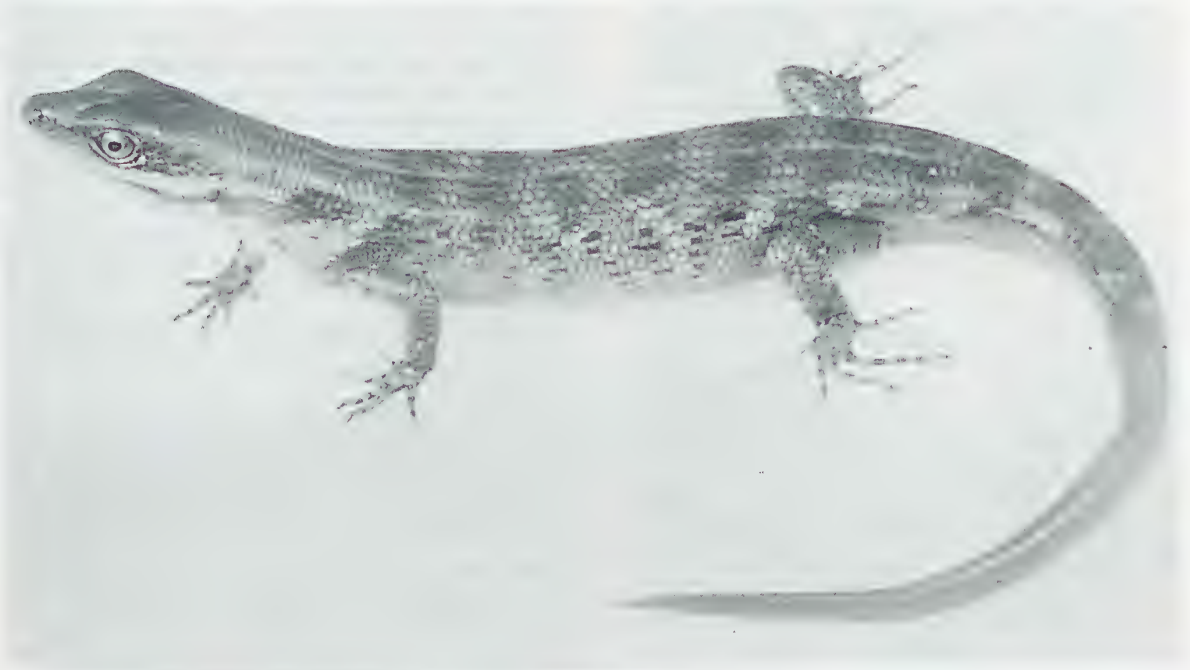


Fig. 25. *Leiolopisma steindachneri* (Bocage) from near Mt Aoupinie forestry camp (500 m), New Caledonia.

secondary temporals, inner most pair in moderate to broad contact or separated by an azygous dorsal scale which usually contacts the parietal narrowly [hence the internuchal scale described by Roux (1913)]; primary temporal usually single, occasionally divided to give 2 equal sized scales; upper secondary temporal usually single, occasionally fragmented anterodorsally producing an additional small scale bordering the parietal; lower secondary temporal usually single, occasionally divided; tertiary temporals 2.

Nasals widely separated, postnasal suture usually absent though a crease from naris to nasoloreal suture may be present (in one individual this forms a distinct suture); anterior loreal semilunar, positioned on posterodorsal margin of nasal and usually failing to contact upper labials (86%, n = 13), infrequently extending its lower edge to contact labials, posterior loreal nearly twice as long as deep, usually (86%, n = 13) contacting both semilunar anterior loreal and nasal anteriorly (though contact with nasal is excluded when anterior loreal projects down to contact upper labials); anterior subocular scales 2–3, subequal; supraciliaries 7(88.5%, n = 13)–8; upper labials 7, with fourth and fifth subocular, but only fifth contacting lower eyelid; postlabials 2; lower labials 6, first 2 contacting postmental; chinshields 3, first pair in broad contact, last pair divided longitudinally.

Lower eyelid with an obvious, centrally located semi-transparent disc, length 27.7–46.1% of total eye length ($\bar{x}$ = 35.4, n = 12).

Ear opening with 2–4 small conical lobules anteriorly.

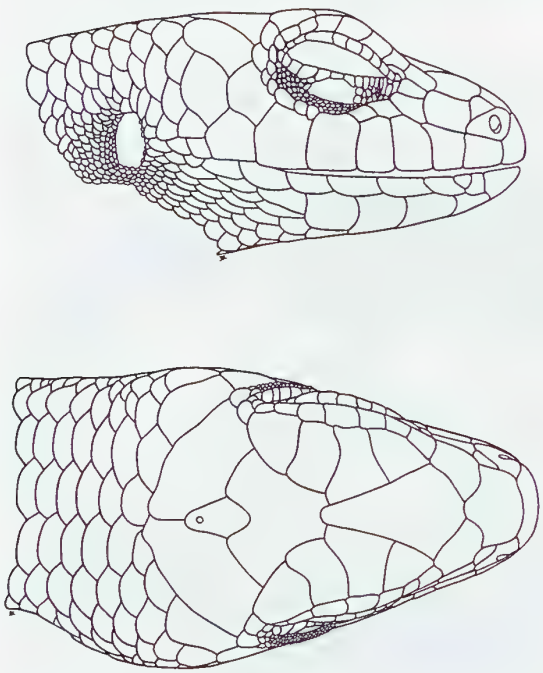


Fig. 26. Lateral and dorsal views of the head of NHMB 7450, neotype of *Lioscincus steindachneri* Bocage.

Body scales smooth, midbody scale rows 34–36 ($\bar{x}$ = 35.7, sd = 0.7, n = 13); paravertebral scales 57–60 ($\bar{x}$ = 58.1, sd = 1.1, n = 13).

Lamellae beneath fourth toe 37–47 ($\bar{x}$ = 42, sd = 2.6, n = 12).

OSTEOLOGY: premaxillary teeth 11 (n = 3); maxillary teeth 25–28 ($\bar{x}$ = 27.2, sd = 1.1, n = 3); dentary teeth 29–32 ($\bar{x}$ = 30.6, sd = 1, n = 3); presacral vertebrae 29; postsacral vertebrae 50–53 ($\bar{x}$ = 51, sd = 1.2, n = 4); phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4 respectively.

COLOUR AND PATTERN: dorsal surface with a series of broad, alternate dark and light transverse bars from nape to basal part of tail; dark bands broadest at dorsolateral edge to give an overall hourglass shape, dark brown and with each scale having a longitudinally aligned black median fleck; lighter interspaces broadly eliptical, nearly enclosed by darker bands, light brown with finer grey to white flecking in region between fore and hindlimbs; head brown above, unmarked. Lateral surface between fore and hindlimbs a continuation of dorsal pattern with dark transverse bars irregular and broken, and light brown to grey flecking on interspaces; forelimb region with a broad black bar extending obliquely from axilla posterolaterally, and a second broad black bar extending posteriorly from supralabials through to ear opening, thence broadening and passing parallel to dark bar from axilla; side of head with a white stripe from subocular upper labial to just above ear opening, partially bordering black bar between jaw and ear, upper labials anterior to eye brown, between white upper labial stripe and top of head dark brown-black. Venter white, medially and occasionally ventrolaterally with a series of transverse grey blotches (continuations of light lateral interspaces); chest and throat spotted with grey. Limbs light brown with random light and dark flecking.

This colour description is based on a series collected in 1978 on Mt Aoupinie on the central ranges. A large series collected by Roux & Sarasin from Mt Ignambi on the north coast ranges differ in that the posterior broad black bar in the region of the forelimb is absent, and the broad black band anterior to that does not continue past level of ear opening.

Distribution and habitats. *Leiolopisma steindachneri* is recorded from the north-east highlands of mainland New Caledonia (Fig. 29).

Roux & Sarasin recorded *L. steindacheri* from moist areas of mountains. Our specimens were from beneath stones at the side of a creek running through thick rainforest ca. 500 m (Fig. 1f). In this habitat, *L. steidachneri* was syntopic with *Marmorosphax tricolor*.

Reproduction. The three adult females collected in December 1978 (SVL 77–88.5 mm) contained 4–8 moderate to large yolked ovarian follicles.

Remarks. The description of *Lioscincus steindachneri* by Bocage (1873b) was based on a single specimen (total

Fig. 27. NHMB 7450, neotype of *Lioscincus steindachneri* Bocage.

length of 197 mm of which the incomplete tail was 110 mm) noted to be in poor condition. The type of *Lioscincus steindachneri* Bocage lodged in the Museum at Lisbon is no longer in existence. As Roux (1913) had examined this specimen and found it to be conspecific with those collected by Roux & Sarasin, a neotype from the collection of Roux & Sarasin has been designated (above) to stabilize the name.

Leiolopisma novaecaledoniae (Parker)

Figs 28–31

Lygosoma (Leiolopisma) novae-caledoniae Parker, 1926: 493.

Type material. HOLOTYPE: *Lygosoma (Leiolopisma) novae-caledoniae* Parker, BM 1946.8.16.15, adult female, SVL 61 mm (Figs 28, 30), upper Houailou River, New Caledonia

Additional material examined. AM R90454, 3 km north of Oue Camme River; AM R77722, creek crossing 1 km north-east of Mt Aoupinie forestry camp by road (500 m), 21°08′S 165°21′E; AM R78349, Houailou airstrip, 21°16′S 165°37′E; ZFMK 25480, 27661, La Foa, 21°43′S 165°52′E.

Diagnosis. *Leiolopisma novaecaleoniae* can be distingished from all other New Caledonian members of the genus by the following combination of characters: frontoparietals fused; supranasals or postnasal suture absent; tertiary temporals fused; subdigital lamellae broad, flat and pale basally, with distal third of fourth toe markedly compressed.

Description. This description is based on five adult specimens.

MEASUREMENTS: maximum SVL 68 mm; distance from axilla to groin 55.4–64.7% of SVL ($\bar{x}$ = 58.8, n = 5); hindlimb length 39–43.8% of SVL ($\bar{x}$ = 41.3, n = 4); tail length ca. 183.7–224.6% of SVL ($\bar{x}$ = 202.8, n = 3).

SCALATION: frontonasal slightly broader than long (W/L 108.9–129%, $\bar{x}$ = 119, n = 4); prefrontals large, narrowly separated or in point contact; frontal longer than broad (W/L 76.2–80.5%, $\bar{x}$ = 78%, n = 4); frontoparietals fused (paired in AM R77722); interparietal distinct; parietals each bordered by a single nuchal and upper secondary temporal scale; primary temporal single; upper and lower secondary temporals single; tertiary temporals fused to form a single scale.

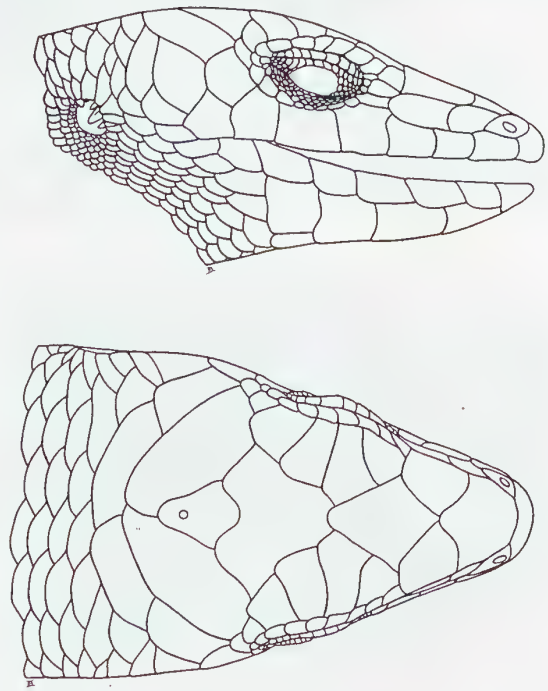


Fig. 28. Lateral and dorsal views of the head of BM 1946.8.16.15, holotype of *Lygosoma novae-caledoniae* Parker.

Fig. 29. Distribution of *Leiolopisma steindachneri* (closed circle) and *Leiolopisma novaecaledoniae* (open star) in New Caledonia.

Nasals widely separated; 2 loreals in a horizontal sequence, anterior near as long as deep, posterior longer than deep and shallower than anterior loreal; anterior suboculars 2–3, anteriormost large, remainder markedly smaller; supraciliaries usually 7 (70%, n = 5), occasionally 6 or 8; upper labials usually 7 (70%, n = 5) with fifth subocular and contacting lower eyelid, occasionally 8 with sixth subocular; postlabials 2; lower labials 6, first 2 contacting postmental; chinshields 3, first pair in broad contact.

Lower eyelid with an obvious, centrally located semi-transparent disc, length 40–49.1% of eye length ($\bar{x}$ = 46.1, n = 4).

Ear opening with a single large obtuse lobule and up to 2 small acute lobules anteriorly.

Body scales tri- to quadricarinate on dorsal to midlateral surface, each dorsal keel interrupting posteriormost edge of scale, number of keels increasing to 5 or 6 towards nape as scales progressively broaden; midbody scale rows 30–34 ($\bar{x}$ = 31.8, sd = 1.2, n = 6); paravertebal scales 56–59 ($\bar{x}$ = 57.7, sd = 1.2, n = 6).

Lamellae beneath fourth toe 21–24 ($\bar{x}$ = 22.1, sd = 0.9, n = 6), broad, flat and pale with no obvious callus over basal two thirds of digit, considerably narrower over distal third.

OSTEOLOGY: premaxillary teeth 11(80%, n = 5)–12; maxillary teeth 23–29 ($\bar{x}$ = 26.3, sd = 2, n = 5); dentary teeth 29–35 ($\bar{x}$ = 31.3, sd = 1.8, n = 5); presacral vertebrae 29 (n = 5); phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4, respectively.

COLOUR AND PATTERN: (in alcohol) dorsal surface brown with a tan to russet tinge; prominent pale hip stripe posteriorly, extending laterally at base of tail; tail with numerous pale flecks above. Lateral surface light brown, mottled with fine light and dark flecks. Hindlimbs above same as dorsum, underneath with a

brown mottle. Venter posterior of forelimbs white with irregular brown spotting ventrolaterally, tending to form transversely aligned bars posteriorly approaching hindlimbs; throat white, lower labials and chinshields dark edged; tail with heavy irregular mottle of light and dark flecks beneath.

In life, lateral surface with a pinkish flush; ventral spotting russet brown; soles of feet and subdigital lamellae light yellow; oral mucosa striking deep blue; iris yellow. Meier (1979a) presents a colour photograph of a live specimen of *L. novaecaledoniae*.

Distribution and habitats. *Leiolopisma novaecaledoniae* is known from five widespread localities on mainland New Caledonia north of ca. 21°50′S (Fig. 29). It occurs in a range of habitats, having been recorded from the edge of moist coastal vine thickets (Fig. 1a,b), and from rocks and boulders bordering lowland and highland streams passing through rainforest (Fig. 1f). Parker (1926) notes that a field tag attached to the holotype indicates it was beaten from a tree.

Reproduction. *Leiolopisma novaecaledoniae* is oviparous: ZFMK 25480 (67.5 mm SVL) and BM 1946.8.16.15 (67.5 mm SVL) both contain four (2/2) enlarged-yolked ovarian follicles; AM R78349 (ca. 51 mm SVL) collected December 1978 contains shelled oviducal eggs but is in such a poor state of preservation that clutch size could not be determined.

Fig. 30. BM 1946.8.16.15, holotype of *Lygosoma novae-caledoniae* Parker.

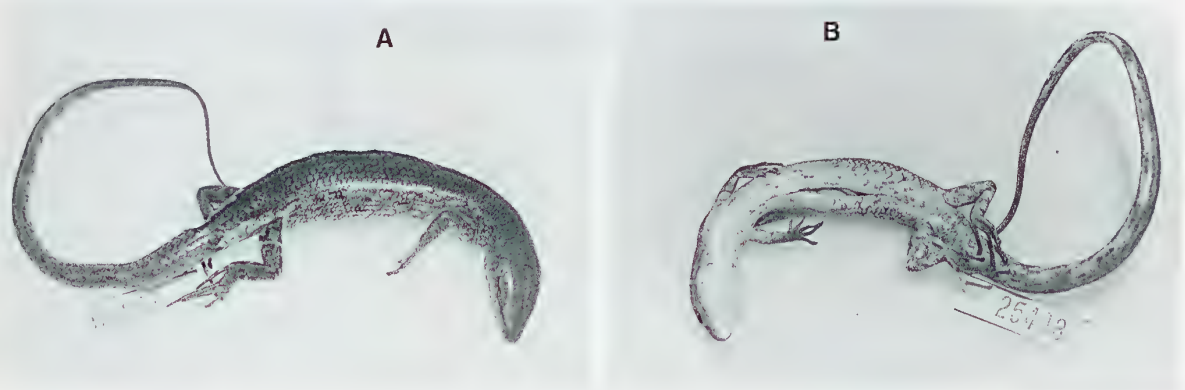


Fig. 31. ZFMK 25408, a specimen of *Leiolopisma novaecaledoniae* (Parker) showing the dorsal colouration **(a)**, and distinctive dark ventral spotting **(b)** of this species.

Genus *Tropidoscincus* Bocage, 1873

Tropidoscincus Bocage, 1873b: 230 (type species *Tropidoscincus aubrianus).*
Sauroscincus Peters, 1879: 149 (type species *Sauroscincus braconnieri).*

Diagnosis. *Tropidoscincus* is a member of the *Eugongylus* group of Greer (1979). It can be distinguished from all other genera in that group by the following combination of characters: frontoparietals fused to form a single scale; supranasals absent but a prominent postnasal suture present; lower eyelid with an obvious, centrally located semi-transparent disc; ear opening large but with moderately small lobules anteriorly; three pairs of mesosternal ribs contacting mesosternum.

Recognized Species. *Tropidoscincus variabilis* (Bavay, 1869); *Tropidoscincus aubrianus* Bocage, 1873b; *Tropidoscincus rohssii* (Andersson, 1908).

Key to Species of *Tropidoscincus*

1. Scales on posterior aspect of thighs overlapping and evenly decreasing in size ventrally. 2

——Scales on posterior aspect of thighs small and juxtaposed, sharply demarcated from large overlapping scales on dorsum of thigh. .... *Tropidoscincus variabilis*

2. Midbody scale rows 32–34. .... *Tropidoscincus aubrianus*

——Midbody scale rows 36–40. .... *Tropidoscincus rohssii*

Tropidoscincus variabilis (Bavay)
Figs 32–34

Tropidolopisma variabilis Bavay, 1869: 26.

Type material. NEOTYPE: *Tropidoscincus variabilis* Bavay, AM R77875, here designated, adult male, SVL 95 mm (Fig. 32, 33), Mt Panie (750 m), New Caledonia, 20°33′S 164°45′E.

Additional material examined. NHMB 19105, Diahot Tal und Col Poraries, 20°17′S 164°18′E; AM R77904, 4 km south of Puebo, 20°25′S 164°37′E; NHMB 7403, 7402, 7406, 7411, 19109, Outbache, 20°26′S 164°38′E; NHMB 7412, Mt Igmambi (600 m), 20°28′S 164°36′E; NHMB 7404, 7414-16, 19107, Tao, 20°33′S 164°48′E; AM R77889, Mt Panie (200 m), 20°33′S 164°45′E; NHMB 7423, Mt Panie (700 m), 20°33′S 164°45′E; AM R77822, Kavatch forestry camp, 20°42′S 164°50′E; AM R77685, 2 km north-east of Mt Aoupinie forestry camp by road (550 m), 21°08′S 165°21′E; AM R77720, 1 km north-east of Mt Aoupinie forestry camp by road (500 m), 21°08′S 165°21′E; AM R77655, Mt Aoupinie forestry camp (500 m), 21°09′S 165°21′E; NHMB 7407, 7417, 19104, Mt Canala (700 m) 21°35′S 165°56′E.

Diagnosis. *Tropidoscincus variabilis* can be distinguished from both *Tropidoscincus aubrianus* and *Tropidoscincus rohssii* by the scales on the posterior

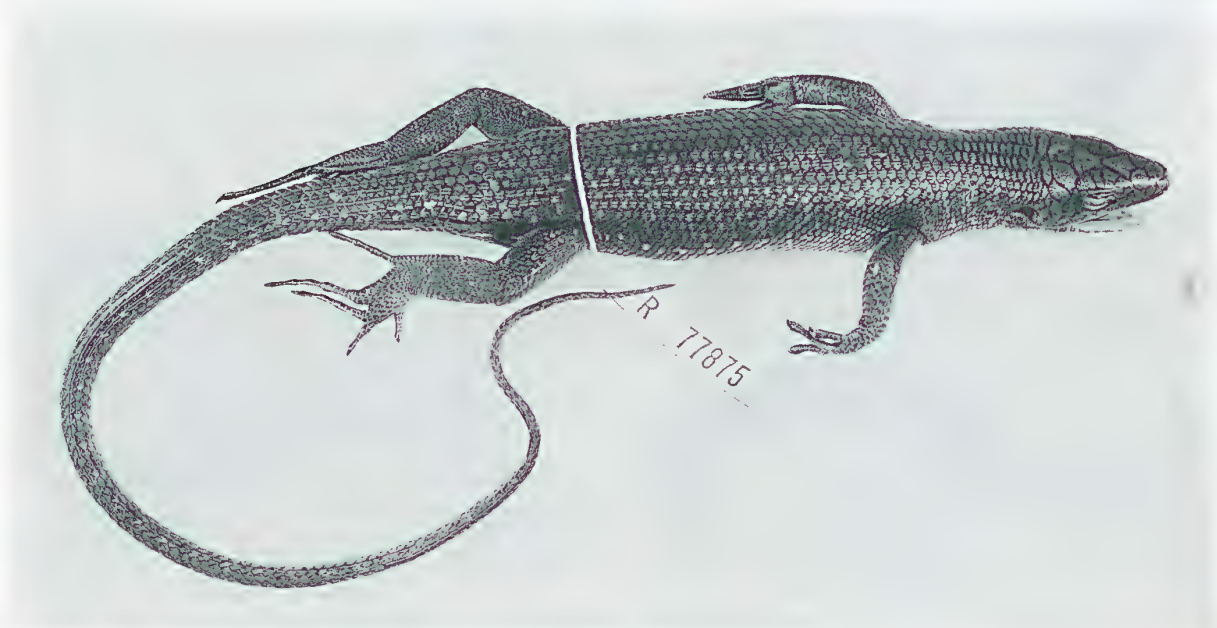


Fig. 32. AM R77875, neotype of *Tropidolopisma variabilis* Bavay.

aspect of the thighs being small, juxtaposed, and sharply demarcated from large overlapping scales on dorsum of thigh, whereas *T. aubrianus* and *T. rohssii* have the scales on the posterior aspect of the thighs overlapping and evenly decreasing in size ventrally. *Tropidoscincus variabilis* is further distinguished from *T. aubrianus* by possesssing more midbody scale rows (36–40 vs 32–34); fewer paravertebral scales (49–58 vs 58–62); more premaxilliary teeth (11 vs 9); juveniles with pale dorsolateral stripe extending only to middorsum vs full length of dorsum to level of hindlimbs in juvenile *T. aubrianus*.

Tropidoscincus variabilis further differs from *T. rohssii* by its generally larger adult body size (maximum SVL 95 mm vs 78 mm).

Description. This description is based on nine juvenile-subadult and 12 adult specimens.

MEASUREMENTS: only adults 66 mm SVL and over i.e. those individuals with full adult colouration, are included in the body measurements.

Maximum SVL 95 mm; distance from axilla to groin 46.9–56.9% of SVL ($\bar{x}$ = 51.8, n = 12); hindlimb length 54.3–63.6% of SVL ($\bar{x}$ = 58.2, n = 12); tail length 240.3% of SVL (n = 1).

SCALATION: frontonasal broad as long (W/L 108.1–150, $\bar{x}$ = 128.4, n = 21); prefrontals large, usually in point contact or narrowly separated (76.2%, n = 21), rarely more widely separated (19%) or broadly contacting; frontal longer than broad (W/L 67.5–81%, $\bar{x}$ = 72.1, n = 21); frontoparietals fused; interparietal distinct; parietals each bordered by a single nuchal and upper secondary temporal scale; primary temporal single; upper and lower secondary temporals single; tertiary temporals 2, rarely 3.

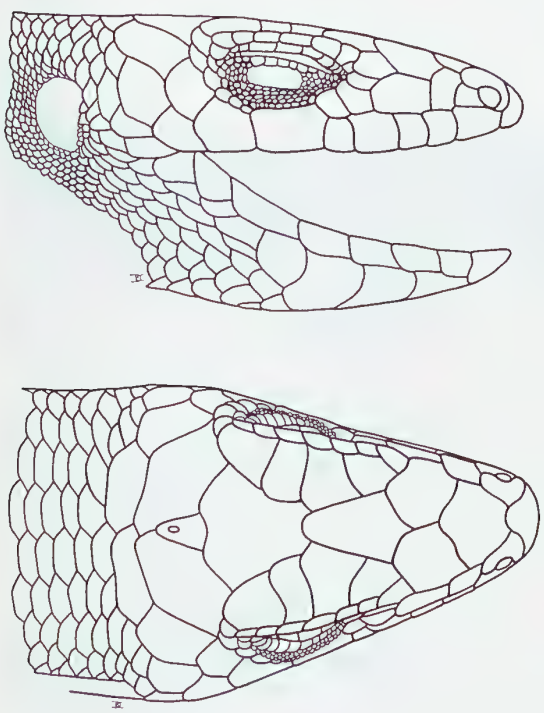


Fig. 33. Lateral and dorsal views of the head of AM R77875, neotype of *Tropidolopisma variabilis* Bavay.

Nasals moderately to widely separated; postnasal suture from top of naris posteriorly to nasoloreal suture, partially dividing nasal to form a postnasal scale; 2 loreals in horizontal sequence, anterior slightly deeper than long, posterior as deep but longer than anterior; anterior subocular usually single (98%, n = 21) and large, rarely followed by a smaller scale; supraciliaries 7 (85.7%, n = 21), rarely 8 (9.5%) or 6; upper labials usually 8 (87.8%, n = 21) with sixth subocular and contacting lower eyelid, rarely 7 (7.3%) or 9 with fifth or seventh respectively subocular; postlabials 2; lower labials usually 6 (74.4%, n = 21), first 2 contacting postmental, less frequently 5 (10.3%) or 7; chinshields 3, first pair in broad contact.

Lower eyelid with an obvious, centrally located, semi-transparent disc, length 36.8–50% of total eye length ($\bar{x}$ = 41.9, n = 17).

Ear opening with usually 2(14.3%, n = 21)–3(71%), rarely 4 or 5, moderately enlarged lobules anteriorly, and numerous small near conical lobules on upper, lower and posterior edges.

Body scales dorsally and laterally tricarinate, each keel interrupting posteriormost edge of scale, number of keels increasing to 5 or 6 towards nape as scales progressively broaden; scales over dorsum of tail tricarinate basally, bicarinate distally; midbody scale rows 36–40 ($\bar{x}$ = 37, sd = 1.6, n = 21); paravertebral scales 49–58 ($\bar{x}$ = 53.3, sd = 2.1, n = 21).

Hindlimbs with bi- and tricarinate scales anterodorsally, scales on posterior aspect of thighs small and juxtaposed, sharply demarcated from large overlapping scales on dorsum of thighs; lamellae beneath fourth toe 36–48 ($\bar{x}$ = 40.9, sd = 3.1, n = 20).

OSTEOLOGY: premaxillary teeth 11 (n = 4); maxillary teeth 28–31 ($\bar{x}$ = 29.7, sd = 1.1, n = 4; dentary teeth 34–39 ($\bar{x}$ = 36.5, sd = 1.8, n = 4); presacral vertebrae 29 (n = 6); postsacral vertebrae 60–62 (n = 2); phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4, respectively.

COLOUR AND PATTERN: marked ontogenetic change from juvenile to adult involves progressive loss of prominent pale dorsolateral and midlateral striping. Colouration descriptions are therefore given for juvenile, subdult and adult phases.

a) Juvenile (31–49 mm SVL). Dorsal surface olive-brown, head darker. Pale dorsolateral stripe (yellow in life) from snout through supraciliaries to just past level of forelimbs, thence fading at middorsum to disappear completely by level of hindlimb. Lateral surface darker than dorsal, obscuring dark postauricular patch which becomes progressively prominent in more mature individuals. Pale midlateral stripe (yellow in life) extending from upper labials posteriorly through to base of ear opening, over forelimb, and along body, prominent to groin in small juveniles but tending to fade

from midbody to groin in larger juveniles. Tail olive-brown with a series of white spots laterally.

b) Subadults (57–65 mm SVL). Dorsal and lateral surface olive-brown, lateral slightly darker, difference between two surfaces less marked than in juveniles; dark postauricular patch brown-black, obvious. Pale dorsolateral stripe less distinct than in juveniles but still extending to forelimb. Pale midlateral stripe extending only to middorsum.

c) Adults (66–94 mm). Dorsum olive-brown overall, head darker with some black spotting above and facially. Mid to lower lateral surfaces slightly lighter than dorsal, particularly about forelimb; dark postauricular patch brown-black, prominent. Pale dorsolateral and midlateral stripes absent, but a midlateral series of cream spots extends from fore to hindlimb and along original portion of tail. Limbs brown with darker flecks. Live adult male specimen (SVL 95 mm) had a bright orange venter posterior to level of ear, ventral surface of tail and hindlimbs duller orange; flanks russet merging lateroventrally with bright orange venter. This colouration was not observed in any of the 3 adult female specimens (SVL 67–88 mm) we collected.

Distribution and habitats. *Tropidoscincus variabilis* is recorded from the north and central east coast and highlands of mainland New Caledonia (Fig. 34). However considering the wide range of habitats from which this species has been collected its apparent absence from the north and central west coasts may be a reflection of inadequate collecting in these regions.

Tropidoscincus variabilis inhabits naueliu woodland (Fig. 1c), coastal scrub (Fig. 1b), lowland rainforest edges, and highland forest clearings (to 700 m). Rankin's field notes also record a number of individuals along the narrow track passing through dense 1–2 metre scrub on an exposed ridge at Mt Panie (700–900 m). *Tropidoscincus variabilis* is sympatric with *T. aubrianus* at Houaliou: both species were observed active by day in isolated sunlit patches in and at the edge of low dense scrub (Fig. 1a,b).

Fig. 34. Distribution of the genus *Tropidoscincus* in New Caledonia: *T. variabilis* (closed circle); *T. aubrianus* (open star); *T. rohssii* (closed square).

Reproduction. Adult females of 88 and 79 mm SVL collected in December 1978 had 2 and 3 enlarged yolked ovarian follicles respectively.

Remarks. Bavay (1869) presumably described *Tropidolopisma variabilis* from more than one specimen as he discussed variability in certain features of scalation and colouration, but only gave dimensions for a single adult individual (30 cm total length).

Bocage (1873) in describing *Tropidoscincus aubrianus* and several other new taxa from New Caledonia was apparently unaware of Bavay's (1869) work. However, in a later review of the New Caledonian reptiles Bocage (1881) recognized *Tropidolopisma variabilis* Bavay and placed *Tropidoscincus aubrianus* Bocage into its synonomy.

Boulenger (1887) redescribed *Lygosoma variabile* (Bavay) from the type of *Sauroscincus braconnieri* Peters which Boulenger incorrectly synonomised with *L. variabilis* (Bavay).

Roux (1913) recognized both *Tropidolopisma variabilis* Bavay and *Tropidoscincus aubrianus* Bocage by redescribing firstly *Lygosoma variabile* and then the subspecies *Lygosoma variabile aubryanum*. It is also of interest to note that Roux interpreted the type description of *Tropidolopisma variabilis* Bavay as possibly also including specimens of *Tropidoscincus aubrianus* Bocage. Roux regarded part of the variability in colouration described by Bavay (1869) for adult specimens of *Tropidolopisma variabilis* (i.e. "generally the ground colour is olive green on top and sometimes mottled and of a dirty grey shade, with an uninterrupted double line made up of brown spots starting at the ear and spreading to the tail") as referable to *Tropidoscincus aubrianus* Bocage.

Tropidoscincus aubrianus Bocage
Figs 34–38

Tropidoscincus aubrianus Bocage, 1873b: 230.
Sauroscincus braconnieri Peters, 1879: 149.

Type material. NEOTYPE: *Tropidoscincus aubrianus* Bocage, NHMB 7424, here designated, adult (sex indeterminate), SVL 107 mm (Figs 36, 37), Pouebo, New Caledonia, 21°21′S 164°29′E. HOLOTYPE: *Sauroscincus braconnieri* Peters, ZMB 9702, juvenile SVL 55 mm (Fig. 36), New Caledonia.

Additional material examined. NHMB 7405, Heinghene, 20°41′S 164°56′E; NHMB 7425, Tiouaka Tal, 20°52′S 165°16′E; AM R78112, Houailou airstrip, 21°16′S 165°37′E; AM R77519-20, La Font Poya, 9 km north-west of Moindou on Bourail road, 21°32′S 165°28′E; NHMB 7426, Brinor.

Diagnosis. *Tropidoscincus aubrianus* can be distinguished from *Tropidoscincus variabilis* by possessing fewer midbody scale rows (32–34 vs 36–40); more paravertebral scales (58–62 vs 49–58); scales on posterior aspect of the thighs overlapping and evenly descreasing in size ventrally whereas *T. variabilis* has the scales on posterior aspect of the thighs small, juxtaposed, and sharply demarcated from large overlapping scales on dorsum of thigh.

Tropidoscincus aubrianus can be distinguished from

Fig. 35. *Tropidoscincus aubrianus* from La Font Poya, New Caledonia.

Tropidoscincus rohssii by possessing fewer midbody scale rows (32–34 vs 36–40); more paravertebral scales (58–62 vs 49–56); fewer lamellae under fourth toe (32–41 vs 34–46).

Juvenile *Tropidoscincus aubrianus* can be distinguished from juveniles of both *Tropidoscincus variabilis* and *Tropidoscincus rohssii* by the pale dorsolateral stripe being prominent in *T. aubrianus* posteriorly to level of the hindlimb instead of fading by middorsum (juvenile *T. rohssii* and *T. variabilis).*

Description. This description is based on three juvenile-subadult and five adult specimens.

MEASUREMENTS: only adults 96 mm SVL and over, i.e. those individuals with full adult colouration are included in the body measurements.

Maximum SVL 121.5 mm; distance from axilla to groin 55.2–58% of SVL ($\bar{x}$ = 56.6, n = 5); hindlimb length 48.3–53% of SVL ($\bar{x}$ = 50.4, n = 4); tail length 180.4% of SVL (n = 1).

SCALATION: frontonasal broader than long (W/L 104.2–151.5, $\bar{x}$ = 126.6, n = 7); prefrontals large, narrowly separated or in point to narrow contact (85.7%, n = 7), rarely in moderate to broad contact; frontal longer than broad (W/L 61–76.9%, $\bar{x}$ = 66.9%, n = 7); frontoparietals fused; interparietal distinct; parietals each bordered by a single nuchal and upper sescondary temporal scale; primary temporal single; upper and lower secondary temporals single; tertiary temporals 2.

Nasals moderately to widely separated; postnasal suture from top of naris posteriorly to nasoloreal suture, partially dividing nasal scale to form postnasal scale; 2 loreals in a horizontal sequence, anterior slightly deeper than long, posterior as deep but longer than anterior; anterior subocular single; supraciliaries 7; upper labials usually 8 (85.7%, n = 7) with sixth subocular and contacting lower eyelid, rarely 9 with seventh subocular; postlabials 2; lower labials usually 6 (71.4%, n = 7), first 2 contacting postmental, less frequently 7 (21.4%) or 5; chinshields 3, first pair in broad contact.

Lower eyelid with an obvious, centrally located semi-transparent disc, length 38.6–45.5% of eye length ($\bar{x}$ = 41.4, n = 6).

Ear opening with 2 (25%, n = 7), 3 (37.5%), 4 (31.3%) or rarely 5 moderately enlarged rounded lobules anteriorly and numerous small rounded lobules on upper, lower and posterior edges.

Body scales tricarinate dorsally to midlaterally in most age classes, each keel interrupting posterior edge of scale, less striate on larger individuals, number of keels increasing to 5 or 6 towards nape as scales progressively broaden; scales over dorsum of tail tricarinate basally, bicarinate distally; midbody scale rows 32–34 ($\bar{x}$ = 33.4, sd = 0.9, n = 7); paravertebral scales 58–62 ($\bar{x}$ = 60, sd = 1.4, n = 7).

Hindlimbs with bi- and tricarinate scales anterodorsally, posteriorly with weakly keeled overlapping scales; lamellae beneath fourth toe 32–41

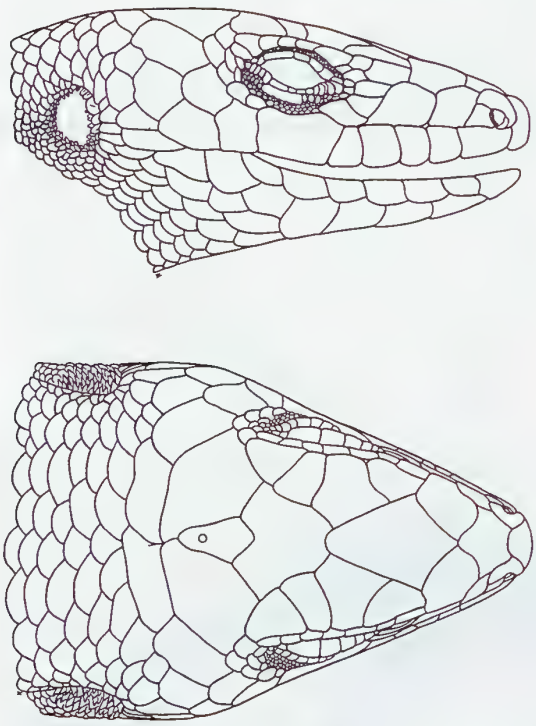


Fig. 36. Lateral and dorsal view of the head of NHMB 7424, neotype of *Tropidoscincus aubrianus* Bocage.

Fig. 37. NHMB 7424, neotype of *Tropidoscincus aubrianus* Bocage.

($\bar{x}$ = 35.6, sd = 2.3, n = 7).

OSTEOLOGY: premaxillary teeth 9 (n = 2); maxillary teeth 25–26 (n = 2); dentary teeth 32–34 (n = 2); presacral vertebrae 29 (n = 7); postsacral vertebrae 59–60 (n = 2); phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4, respectively.

COLOUR AND PATTERN: marked ontogenetic changes in colouration occur in this species. Juveniles possess distinctive pale dorsolateral and midlateral stripes and paravertebral patterns which disappear with maturity, hence description of colouration is divided into juvenile, subadult and adult sections.

a) Juvenile (54–55 mm SVL, n = 2). Dorsal surface brown with faint olive tinge and dark longitudinally aligned flecks paravertebrally; head brown, unmarked. Pale dorsolateral stripe cream, prominent and extending from naris posteriorly to just past level of hindlimb. Lateral surface dark brown uppermost with alternate light and dark flecking along dorsolateral border; pale midlateral stripe cream, prominent and extending from labials posteriorly through base of ear opening and over forelimb to level of hindlimb. Tail overall brown with darker bands laterally not fully encircling tail.

b) Subadult (single specimen 68 mm SVL). Dorsal surface brown with prominent dark paravertebral flecking. Pale dorsolateral stripe cream, extending from naris to just past level of forelimbs. Lateral surface with pale midlateral stripe confined to labials and side of head, not discernable beyond ear opening; upper lateral surface a broken mottle of dark brown with lighter flecks, clearly differentiated anteriorly by light dorsolateral stripe.

c) Adults (SVL 96–107 mm). Dorsal surface with broad dark paravertebral stripes or series of dark flecks, extending from nape to coalesce just past hindlimbs, and thereby enclosing lighter vertebral zone; large adults (SVL 116–121.5 mm) show progressive loss of paravertebral striping which merges with lighter vertebral stripe. Upper lateral surface mid brown, well defined from laterodorsal zone above. Tail predominately light brown.

Live adult male (121.5 mm SVL) had orange flush ventrally posterior of forelimbs, most prominent about vent; pinkish grey flush beneath tail.

Distribution and habitats. *Tropidoscincus aubrianus* occurs in the north-east, central east, and central west of mainland New Caledonia (Fig. 34). It inhabits open woodland of lowland hills on the west coast, and edge of coastal vine thicket at Houailou on the east coast (Fig. 1a,b).

Remarks. Bocage (1873) described *Tropidoscincus aubrianus* (n. gen., n. sp.) from two specimens (an adult 28 cm total length, a juvenile 9 cm total length with a broad white midlateral stripe). Bocage did not refer to Bavay's (1869) description of *Tropidolopisma variabilis*. It seems Bocage was initially unaware of Bavay's prior work but in a later series of short notes on the New Caledonian herpetofauna Bocage (1881) placed *Tropidoscincus aubrianus* in the synonymy of *Tropidolopisma variabilis* Bavay.

In redescribing *Lygosoma variabile,* Roux (1913) also examined one of the specimens described as *Tropidoscincus aubrianus* by Bocage (adult specimen only) and *Sauroscincus braconnieri* by Peters, and subsequently recognised *T. aubrianus* Bocage as a subspecies of *L. variabile,* and *S. braconnieri* Peters as a synonym of the nominate form of *L. variabile*. Roux comments that specimens referable to *Lygosoma variabile aubryanum* were possibly used by Bavay (1869) in describing *Tropidolopisma variabilis* Bavay. However this inference of a composite type series for *T. variabilis* Bavay by Roux was based on the original description of *T. variabilis* (see *T. variabile* — remarks) rather than examination of Bavay's material. Roux also states that

Fig. 38. ZMB 9702, holotype of *Sauroscincus bracconieri* Peters.

the adult specimen described by Bocage as *Tropidoscincus aubrianus* conforms to the three adult females in the collections made by Roux & Sarasin in 1911.

The type of *Sauroscincus braconnieri* Peters has been examined. Boulenger (1887) and Roux (1913) are here considered incorrect in placing it in the synonymy of *Lygosoma variabile*. The colouration of this specimen (ZMB 9702) is similar to a juvenile (NHMB 7405, SVL 54 mm) collected by Roux & Sarasin from Heinghene, and in which pale dorsolateral and midlateral stripes both continue to the level of the hindlimb. Both the type of *Sauroscincus braconnieri* Peters and juvenile specimen collected by Roux & Sarasin (NHMB 7405, but not mentioned by Roux in the description of *Lygosoma variabile aubryanum)* have 34 midbody scale rows. These features of colouration and scalation serve to separate juvenile *Tropidoscincus aubrianus* from its cogeners. *Sauroscincus braconnieri* Peters is here considered a synonym of *Tropidoscincus aubrianus*.

Tropidoscincus rohssii (Andersson)
Figs 34, 39–41

Lygosoma rohssii Andersson, 1908: 4.

Type material. LECTOTYPE: *Lygosoma rohssii* Andersson, here designated, largest of 3 syntypes NHMG 994, adult male, SVL 80 mm (Figs 39, 40), New Caledonia.

Additional material examined. NHMB 7408-09, 7418-19, 19106, 19108, Ngoi Tal (200 m), 21°49′S 166°36′E; AM R116031-35, La Riviere Bleu, 22°06′S 166°40′E; NHMB 7410 and 7420, Yate, 7421, Mt Yate (600 m), AM R78231, La Fause Yate bridge, 22°09′S 166°54′E; AM R78219, base of Mt Gouemba road, near Yate, 22°10′S 166°57′E; AM R78245, 2 km west of Plum turnoff on Mt Dore road, 22°17′S 166°37′E; NHMB 7422-23, Plaine des Lacs (200 m); NHMG 994 (remaining 2 specimens of syntype series), New Caledonia.

Diagnosis. *Tropidoscincus rohssii* can be distinguished from *T. variabilis* by its generally smaller adult body size (maximum SVL 78 mm vs 95 mm), and scales on the posterior aspect of thighs overlapping and evenly decreasing in size ventrally whereas *T. variabilis* has the scales on posterior aspect of thighs small, juxtaposed, and sharply demarkated from large overlapping scales on dorsum of thigh.

Tropidoscincus rohssii is distinguished from *T. aubrianus* by possessing more midbody scale rows (36–40 vs 32–34); fewer paravertebral scales (49–56 vs 58–62); more lamellae beneath the fourth toe (34–40 vs 32–41); more pronounced dorsal keels; more premaxillary teeth (11 vs 9); pale dorsolateral stripes in juvenile *T. rohssii* prominent anteriorly thence tending

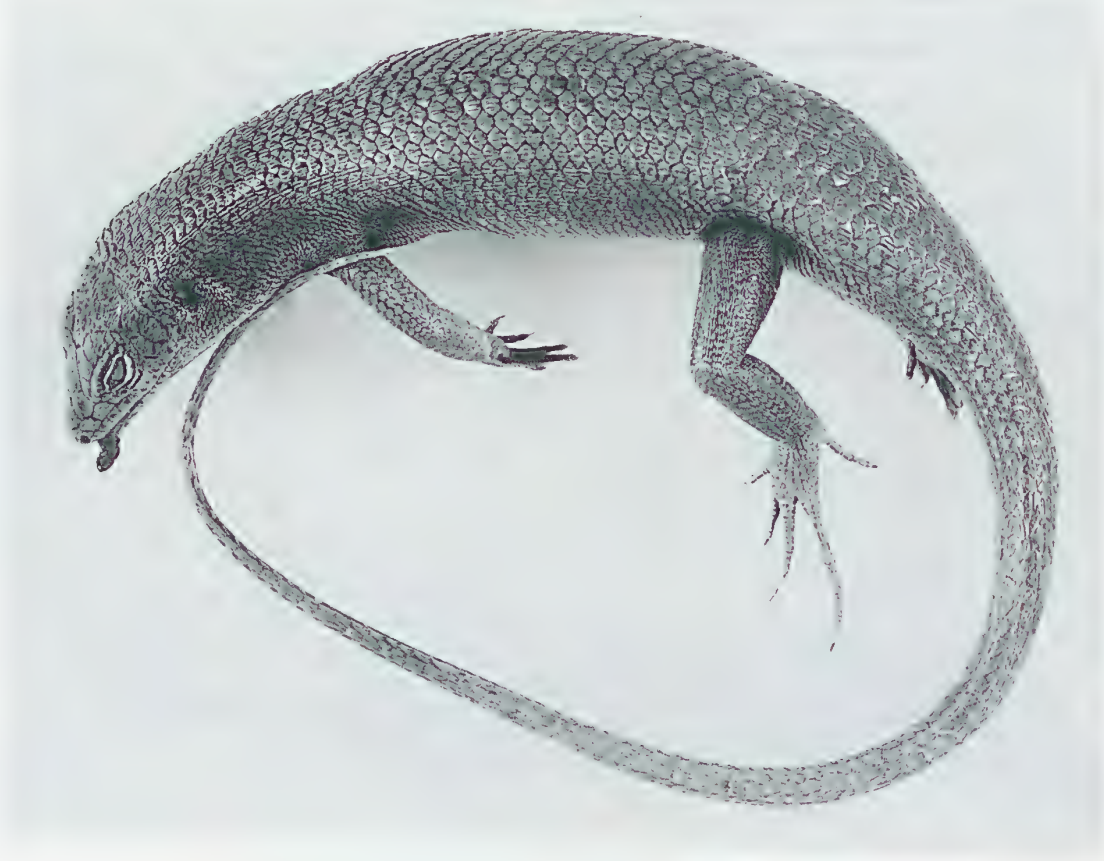


Fig. 39. Lectotype of *Lygosoma rohssii* Andersson, largest of 3 syntypes.

to fade by middorsum whereas the pale dorsolateral stripe is prominent from naris to level of hindlimb in juvenile *T. aubrianus*.

Description. This description is based on six juvenile-subadult and 11 adult specimens.

MEASUREMENTS: only adults 64 mm SVL and over, ie. those individuals with full adult colouration, are included in the body measurements.

Maximum SVL 78 mm; distance from axilla to groin 42.5–53.7% of SVL ($\bar{x}$ = 49.2, n = 11); hindlimb length 54.5–64.2% of SVL ($\bar{x}$ = 58.5, n = 11); tail length 251.8% of SVL (n = 1).

SCALATION: frontonasal broad as long (W/L 120–142.8, $\bar{x}$ = 130.5, n = 14); prefrontals large, usually in point contact or narrowly separated (92.9%, n = 14), rarely more widely separated; frontal longer than broad (W/L 66.6–78.3%, $\bar{x}$ = 76, n = 14); frontoparietals fused; interparietal distinct; parietals each bordered by a single nuchal and upper secondary temporal scale; primary temporal single; upper and lower secondary temporals single; tertiary temporals 2, rarely fused to form a single scale.

Nasals moderately to widely separted; postnasal suture from top of naris posteriorly to nasoloreal suture, partially dividing nasal scale to form a postnasal scale; 2 loreals in horizontal sequence, anterior square and slightly deeper than long, posterior as deep but longer than anterior; anterior subocular single; supraciliaries 7 (96.4%, n = 14), rarely 8; upper labials usually 8 (89.3%, n = 14) with sixth subocular and contacting lower eyelid, rarely 7 (7.1%) or 9 with fifth or seventh subocular respectively; postlabials 2; lower labials usually 6 (60.7%, n = 14), first 2 contacting postmental, less frequently 5 (21.4%) or 7; chinshields 3, first pair in broad contact.

Lower eyelid with an obvious, centrally located semi-transparent disc, length 37.2–45.5% of total eye length ($\bar{x}$ = 41.8, n = 12).

Ear opening with 3(50%, n = 14)–4(46.4%), rarely 5, moderately enlarged rounded lobules anteriorly and numerous small rounded lobules on upper, lower and posterior edges.

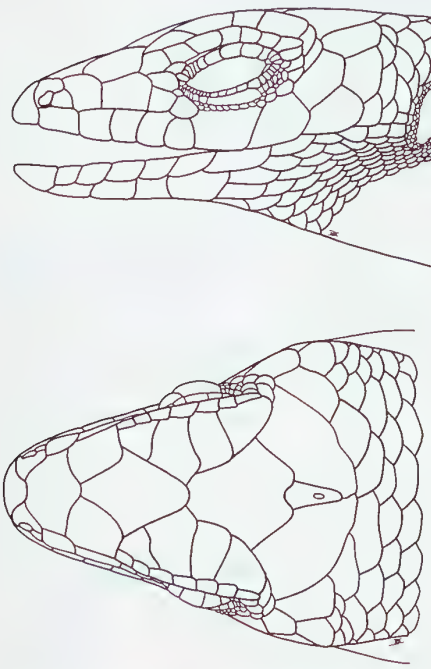


Fig. 40. Lateral and dorsal views of the head of the lectotype of *Lygosoma rohssii* Andersson, largest of 3 syntypes.

Fig. 41. *Tropidoscincus rohssii* from La Riviere Bleu showing the pale dorsolateral and lateral striping present on juveniles of this species.

Body scales dorsally and laterally tricarinate, each keel interrupting posteriormost edge of scale, number of keels increasing to 5 or 6 towards nape as scales progressively broaden; midbody scale rows 36–40 ($\bar{x}$ = 37.4, sd = 1.4, n = 14); paravertebral scales 49–56 ($\bar{x}$ = 52.9, sd = 2, n = 13).

Hindlimbs with bi- and tricarinate scales anterodorsally, scales on posterior aspect of thighs overlapping and evenly descreasing in size ventrally; lamellae beneath fourth toe 34–46 ($\bar{x}$ = 39.5, sd = 2.4, n = 14).

OSTEOLOGY: premaxillary teeth 11 (n = 2); maxillary teeth 25–28 ($\bar{x}$ = 26.2, sd = 1.3, n = 2); dentary teeth 30–33 ($\bar{x}$ = 31.5, sd 1.1, n = 2); presacral vertebrae 29 (n = 7); postsacral vertebrae 60–62 (n = 2); phalangeal formula for manus and pes 2.3.4.5.3. and 2.3.4.5.4, respectively.

COLOUR AND PATTERN: very similar to *T. variabilis* and featuring same ontogenetic loss of prominent pale dorsolateral and midlateral striping from juvenile to adult.

Distribution and habitats. The majority of records for *Tropidoscincus rohssii* are from the southern, western and eastern coasts of mainland New Caledonia (Fig. 34). Roux & Sarasin also recorded it from the Plaine de Lacs region (Fig. 1d).

Tropidoscincus rohssii inhabits open forest and lowland rainforest edges (Fig. 1e).

Remarks. Andersson's concept of *Lygosoma variabile* (Bavay) was based entirely on features of juveniles of that species (small and with pale "longitudinal streaks") and therefore the diagnostic features Andersson proposed to differentiate *Lygosoma rohssii* were typical also for adult *Tropidoscincus variabilis* (Bavay).

Marmorosphax n. gen.

Type species. *Lygosoma tricolor* Bavay, 1869: 17.

Diagnosis. *Marmorosphax* can be distinguished from all other genera in the *Eugongylus* group of Greer (1979) by the following combination of characters: frontoparietals fused; supranasal scale or postnasal suture absent; anterior loreal either contacting upper labials narrowly (*M. euryotis)* or present as a semilunar scale failing to contact upper labials (*M. tricolor);* subocular scale row complete; lower eyelid with an obvious, centrally located semi-transparent disc; ear lobules very small, barely distinguishable from small, blunt conical scales around upper, lower and posterior edges of ear opening; premaxillary teeth 13.

Recognized species. *Marmorosphax tricolor* (Bavay, 1869); *Marmorosphax euryotis* (Werner, 1909).

Etymology. The name *Marmorosphax* combines the Greek for marbled *(marmoros)* and throat *(sphax)* to describe the distinctive dark and light pattern present on the throat of both species in the genus.

Remarks. *Marmorosphax tricolor* (Bavay) is well represented in Museum collections and reasonably well documented in morphology and to a lesser degree behaviour (Roux 1913). By contrast, the only other species in the genus, *Marmorosphax euryotis,* is poorly represented in Museum collections and virtually nothing is known of its distribution or habits. *Lygosoma euryotis* Werner is included in *Marmorosphax* because it shares the diagnostic adult features of the genus. Unfortunately it is not known if it also shares the male ontogenetic colour change of the type species and if it has the peculiar, habits and habitat preference of this species.

Marmorosphax tricolor (Bavay)

Figs 42–46

Lygosoma tricolor Bavay, 1869: 17.

Type material. NEOTYPE: *Lygosoma tricolor* Bavay, AM R77750, here designated, adult male, SVL 53 mm (Figs 43, 44), summit of Mt Aoupinie (1086 m), New Caledonia, 21°11′S 165°16′E.

Additional material examined. NHMB 7427-28, Mt Ignambi (700 m), 20°28′S 164°36′E; AM R77848-52 (300–500 m), 77860-63 (500–600 m), 77865-69 (200–300 m), 77876 (710 m), 77890-91 (770 m), Mt Panie, 20°33′S 164°45′E; AM R77807-08, creek behind Kavatch forestry camp, 20°42′S 164°50′E; AM R77612-37, 77678-83, 77765-70, Mt Aoupinie forestry camp (500 m), 21°09′S 165°20′E; AM R77693-98 2 km north-east of Mt Aoupinie forestry camp by road (500 m), 21°08′S 165′21′E; AM R77699-706, 77788-99, 1 km north-east of Mt Aoupinie forestry camp by road (500 m), 21°08′S 165′21′E; AM R77729-31, 3 km north-east of Mt Aoupinie forestry camp by road (500 m), 21°07′S 165°22′E; AM R77747-49, 77751-54, summit of Mt Aoupinie (1086 m), 21°11′S 165°16′E; AM R77764, 6 km from summit of Mt Aoupinie by road (800 m), 21°11′S 165°16′E; NHMB 7438-39, Boreare, 21°22′S 165°57′E; AM R77532-40, 21 km north-west of Poya intersection on Bourail to Heinghene Road, 21°24′S 165°26′E; NHMB 7443-45, La Foa (100 m), 21°43′S 165°49′E; NHMB 7431-33, Mt Canala (700 m), 21°32′S 165°57′E; NHMB 7436-37, Negropo, 21°32′S 165°54′E; AM R78133, 78149, base of Mt Gouemba road, near Yate, 22°10′S 166°57′E; QM J44006, Mt Koghis (400 m), 22°10′S 166°32′E; QM J43999, Foret Thy Reserve (150 m).

Diagnosis. *Marmorosphax tricolor* can be distinguished from the only other species in the genus, *Marmorosphax euryotis,* by: each parietal bordered by a single upper secondary temporal and single nuchal (vs bordered by a single upper secondary temporal and several more or less uniformly sized scales not noticeably larger than dorsal scales of nape); more midbody scale rows (36–42 vs 32); more paravertebral scales (63–75 vs 52–55).

Description. The measurements and scalation for this description are based on a sample of 10 subadult and 60 adult (including neotype) specimens from Mt Aoupinie, and colouration on all specimens examined.

MEASUREMENTS: males begin to develop features of colouration distinct from adult females around a size 50 mm SVL. The smallest reproductively active females also are of this size. Only those specimens of 50 mm

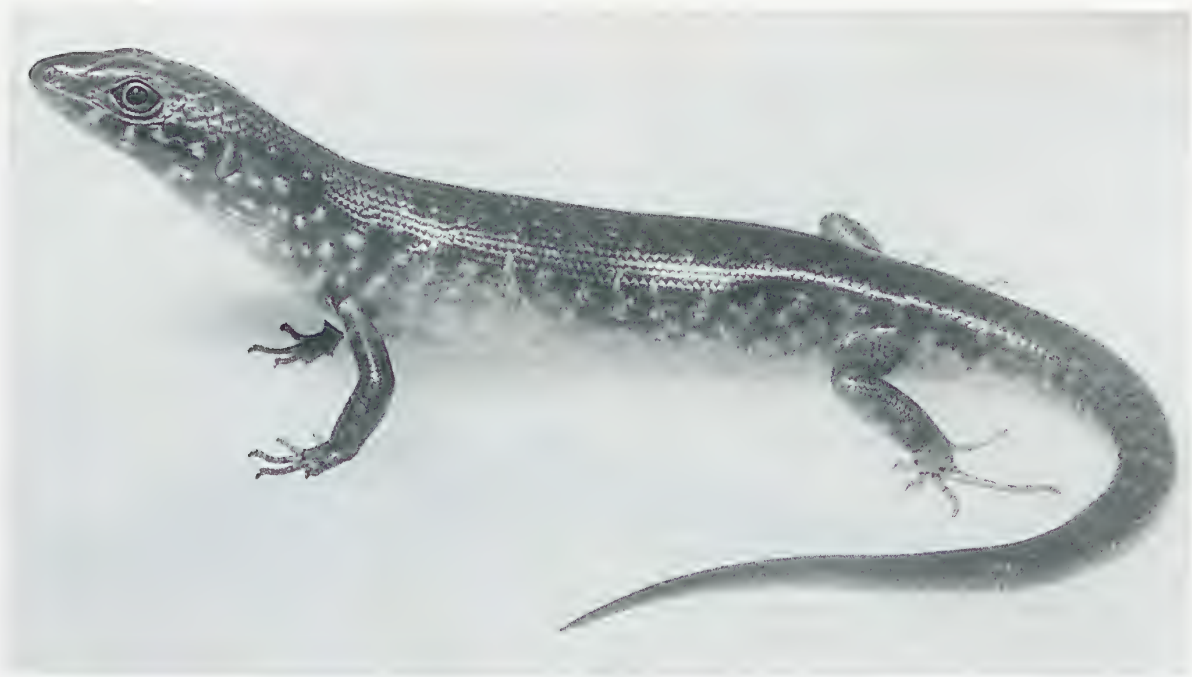


Fig. 42. *Marmorosphax tricolor* from Mt Aoupinie forestry camp (500 m), New Caledonia.

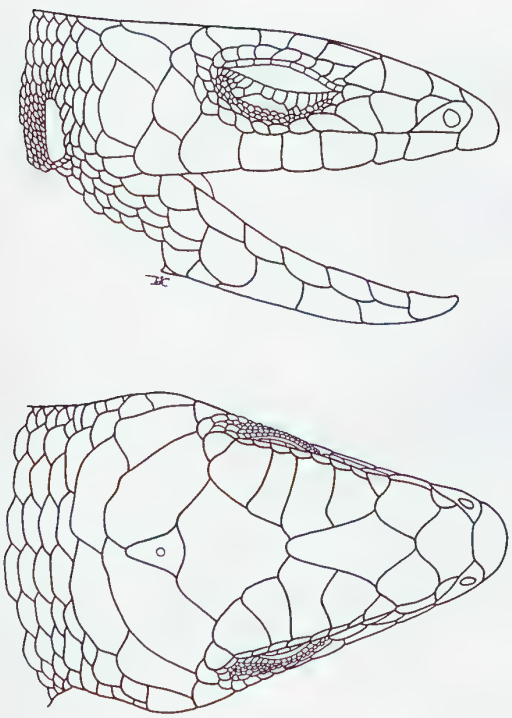


Fig. 43. Lateral and dorsal views of the head of AM R77750, neotype of *Lygosoma tricolor* Bavay.

SVL and over are included in the following body measurements.

Maximum SVL 66 mm; distance from axilla to groin 46.7–64.7% of SVL ($\bar{x}$ = 54.7, n = 60); hindlimb length 37.1–50% of SVL ($\bar{x}$ = 43.7, n = 58); tail length ca. 114–163.5% of SVL, ($\bar{x}$ = 141.2, n = 25).

SCALATION: frontonasal broader than long (W/L 112.5–140.9%, $\bar{x}$ = 125.4, n = 64); prefrontals large, usually narrowly separated (71.4%, n = 65), less frequently moderately separated (4.2%) or in point contact; frontal longer than broad (W/L 60–74.5%, $\bar{x}$ = 66.9, n = 63); frontoparietals fused; interparietal distinct; parietals each bordered by a nuchal and upper secondary temporal scale; primary temporal single; upper and lower secondary temporals single; tertiary temporals 2.

Nasals widely separated; anterior loreal a semilunar scale positioned on posterodorsal margin of nasal and failing to contact upper labials; posterior loreal as long as deep, and anteriorly contacting both semilunar anterior loreal and nasal; supraciliaries usually 8 (84.3%, n = 67) occasionally 7 (3.7%) or 9; upper labials 7 (99.2%, n = 67) with fifth subocular, rarely 6 or 8, with fourth or sixth respectively subocular but separated from lower eyelid by a complete row of subocular scales; lower labials 6 (94%, n = 67) rarely 5 or 7, first 2 contacting postmental; chinshields 3, first pair in broad contact, third pair divided.

Lower eyelid with an obvious, centrally located semi-transparent disc, length 32.7–42% of total eye length ($\bar{x}$ = 37.8, n = 60).

Ear opening with no obvious enlarged lobules at the edges.

Body scales with 3–5 fine keels dorsally and 3–4 weaker keels laterally, failing to interrupt posterior edge of scale; midbody scale rows 36–42 ($\bar{x}$ = 39.9, sd = 1.4, n = 70); paravertebral scales 63–75 ($\bar{x}$ = 68.9, sd = 2.7, n = 69).

Lamellae beneath fourth toe 26–33 ($\bar{x}$ = 30, sd = 1.4, for n = 66).

OSTEOLOGY: premaxillary teeth 13 (96.5%, n = 28), rarely 12 or 14; maxillary teeth 23–28 ($\bar{x}$ = 25.7, sd = 1.3, n = 30); dentary teeth 27–34 ($\bar{x}$ = 30.6, sd = 1.5, n = 22); presacral vertebrae 29; postsacral vertebrae 44–45 (n = 2); phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4, respectively.

COLOUR AND PATTERN: marked sexual dimorphism in adults, the most obvious features being: females darker on dorsal and lateral surfaces than males; females with dorsal and lateral colouration sharply demarcated (gradual change in males); intense contrast

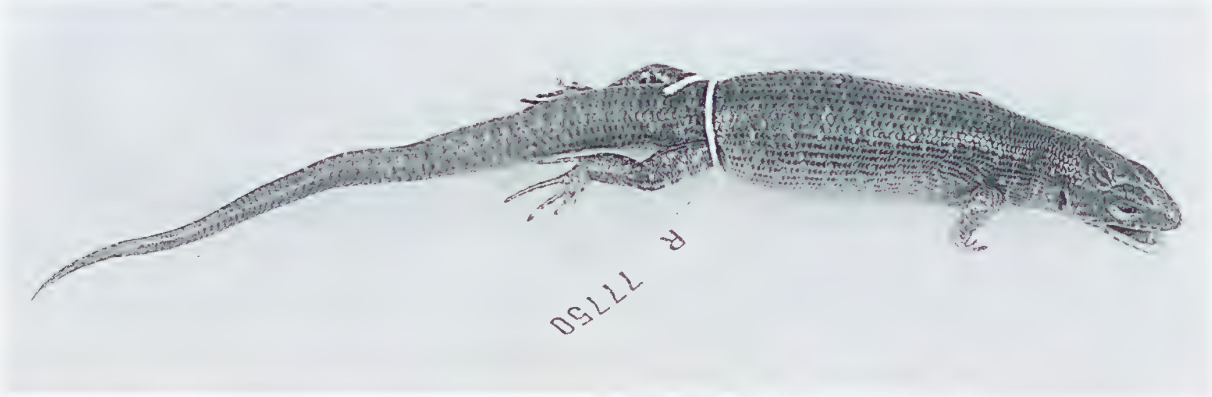


Fig. 44. AM R77750, neotype of *Lygosoma tricolor* Bavay.

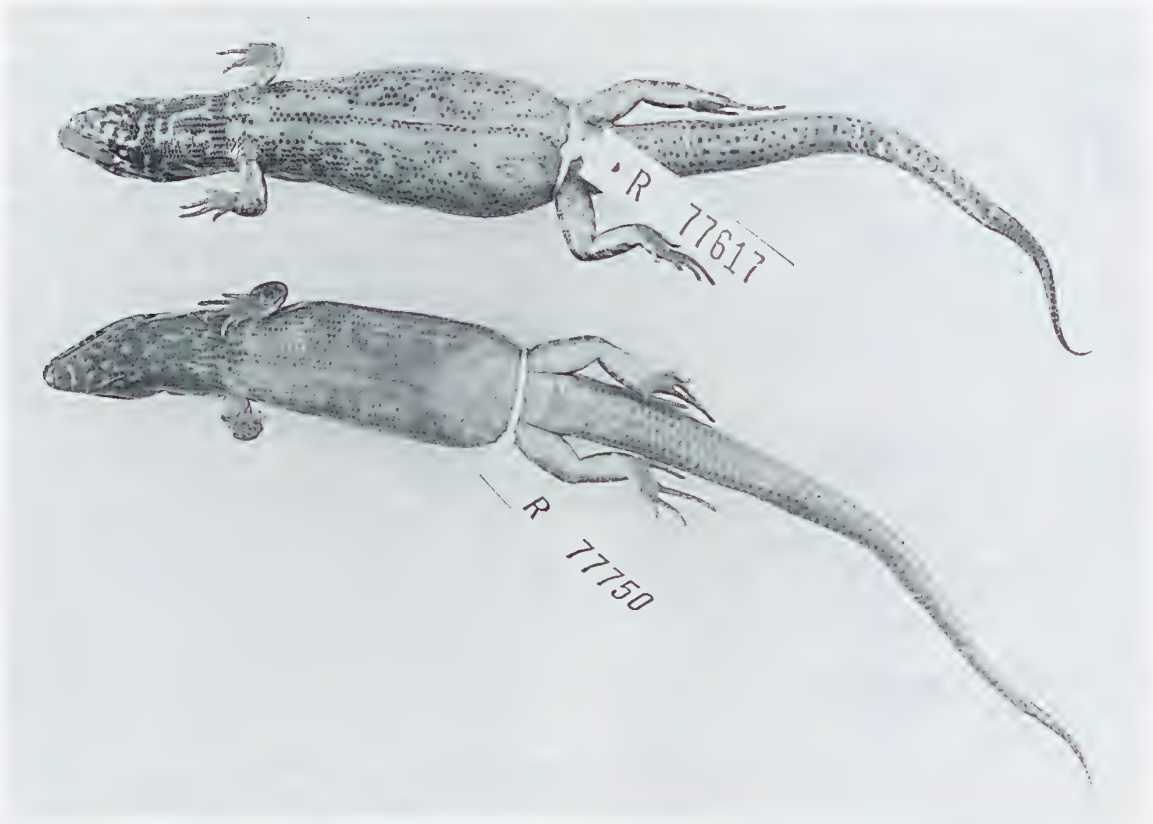


Fig. 45. AM R77750 an adult male, and AM R77617 an adult female of *Marmorosphax tricolor* showing sexual dimorphism in venter colouration.

between light and dark areas on throat in females (diffuse contrast in males).

Venter posterior of forelimb in both sexes either immaculate white or variably dark flecked with several intermediate stages, occasionally also with dark transverse bars and/or a longitudinally aligned bar at mid venter; females overall more heavily marked ventrally.

a) Adult males. Dorsal surface light to mid brown, comprising a mixture of light and dark flecks, continuing onto upper lateral surface with white flecks tending to form spots, thence paling over remainder of lateral surface. Throat a diffuse mottle of grey and dull cream blotches (Fig. 45a).

b) Adult females. Dorsal surface dark brown, sharply demarcated from dark brown-black upper lateral surface, most prominent anterior to forelimb. Mid to lower lateral surface grey-brown; white spotting to lateral surface distinct anteriorly, tending to be obscure posteriorly. Throat a mottle of black and grey blotches, boldly contrasting and sharply defined (Fig. 45b).

c) Subadults and Juveniles. Similar to adult females. Of 29 subadult and juvenile specimens examined four showed some degree of intermediacey between adult male and female colour pattern. Two subadult males (SVL 52–53 mm) tended towards female colour pattern having bold throat markings but poorly defined upper lateral markings more typical of adult males. Two subadult males (SVL 50–51 mm) tended towards the adult male colour pattern but had throat and upper lateral marking well defined and more boldly contrasting than usual in adult males.

Distribution and habitats. *Marmorosphax tricolor* has been recorded largely from the central and east coast highlands of mainland New Caledonia, and also from La Foa on the west coast (Fig. 46). It inhabits the interior of closed rainforest habitat (Figs 1f,g). Individuals were collected from beneath rocks and logs on forest floor, and beneath similar debris at recently cleared (logged) sites surrounded by forest. Although common in this sheltered habitat it was only observed

Fig. 46. Distribution of the genus *Marmorosphax* in New Caledonia: *M. tricolor* (closed circles); *M. euryotis* (open star).

active during completely overcast conditions with mist and fine rain. At one locality beside a flowing creek, in heavy rain but moderately warm conditions, individuals were very active when uncovered and showed no hesitation in entering the water.

Reproduction. *Marmorosphax tricolor* is viviparous. A female (61.1 mm SVL) held in captivity produced four live young in late January 1979 all of approximately 25 mm SVL.

Adult females (50.5–60 mm SVL) from series collected in December 1978 from localities on the east coast contained 1–5 embryos. Litter size increased with female SVL (larger females > 59 mm SVL, mode of 3 and 4, n = 13 vs smaller females < 59 mm SVL mode of 3, n = 22).

Remarks. Boulenger (1887) incorrectly placed *Lioscincus steindachneri* Bocage in the synonomy of *Lygosoma tricolor* Bavay. Roux (1913) later recognized *L. steindachneri* Bocage as distinct.

Marmorosphax euryotis (Werner)

Figs 46–48

Lygosoma euryotis Werner 1909: 271.

Type material. HOLOTYPE: *Lygosoma euryotis* Werner, MRHN 822, SVL 34 mm (Figs 47, 48), Isle of Pines, New Caledonia.

Additional material examined. QM J37441, Ouaiéme via Hienghene, 20°37′S 164°51′E.

Diagnosis. *Marmorosphax euryotis* can be distinguished from the only other species in the genus, *Marmorosphax tricolor,* by: each parietal bordered by several more or less uniform sized scales not noticably larger than dorsal scales (vs bordered by a single upper secondary temporal and single nuchal); fewer midbody scale rows (32 vs 36–42); fewer paravertebral scales (52–55 vs 63–75).

Description. MEASUREMENTS: maximum SVL 40 mm; distance from axilla to groin 50–51.8% of SVL ($\bar{x}$ = 50.9, n = 2); hindlimb length 44.1–44.4% of SVL ($\bar{x}$ = 44.2, n = 2).

SCALATION: frontonasal broader than long (W/L 125–142.8%, $\bar{x}$ = 133.9, n = 2); prefrontals moderately large, moderately separated; frontal longer than wide (W/L 78.4–80%, $\bar{x}$ = 79.2, n = 2); frontoparietals fused; interparietal distinct; parietals each bordered by 2 more or less equally sized nuchal scales and a single upper secondary temporal; nuchal scales bordering parietal no larger than surrounding dorsal scales, and with either of inner nuchal scales only narrowly contacting parietal; primary temporal single; upper and lower secondary temporals single; tertiary temporals 2.

Nasals widely separated; anterior loreal narrow, deep as nasal (except right side of J.37441 where it is semilunar and very narrowly separated from first upper labial thereby allowing narrow contact between posterior loreal and nasal); posterior loreal almost as long as deep, noticeably shallower than anterior loreal; supraciliaries 7; upper labials 7 with fifth subocular, separated from lower eyelid by complete subocular row; postlabials 2; lower labials 6, first 2 contacting postmental; chinshields 3, first pair in broad contact.

Lower eyelid with obvious, centrally located semi-transparent disc, length approximately 45–48.9% eye length.

Ear opening with up to 3 slightly enlarged conical lobules anteriorly, recessed behind scales bordering anterior margin of ear, remainder of ear margin with small conical lobules.

Dorsal and upper lateral body scales with 3 keels, rarely interrupting posterior edge of scale, tending instead to produce a wavy edge, number of keels increasing towards nape but becoming less pronounced;

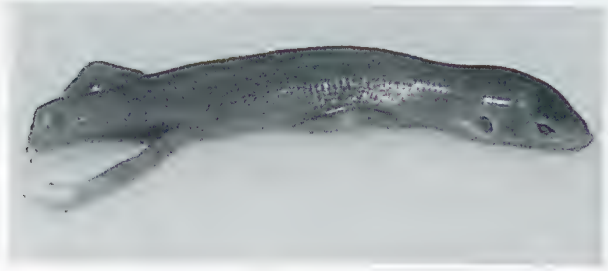


Fig. 47. MRNH 822, holotype of *Lygosoma euryotis* Werner.

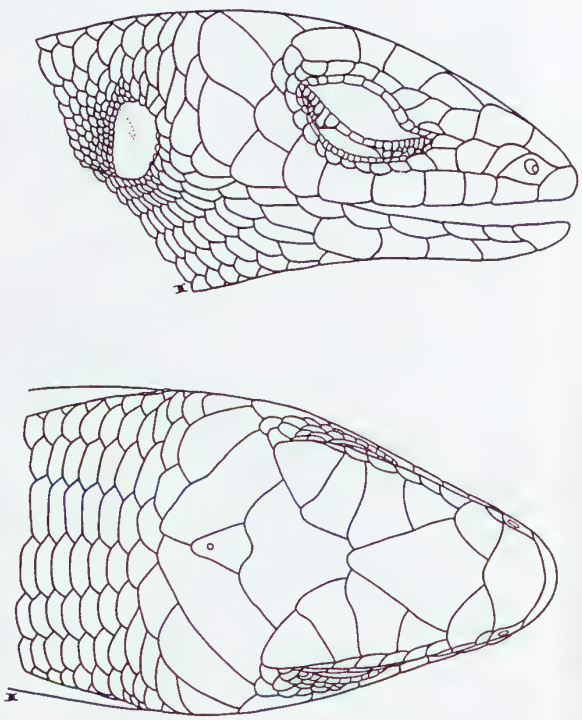


Fig. 48. Lateral and dorsal views of the head of MRNH 822, holotype of *Lygosoma euryotis* Werner.

midbody scale rows ca. 30–32 (n = 2); paravertebral scales 52–55 (n = 2).

Lamellae beneath fourth toe 31–35 (n = 2).

OSTEOLOGY: premaxillary teeth 13 (n = 1); maxillary teeth 22–23 (n = 1); dentary teeth 25 (n = 1); presacral vertebrae 29 (n = 1); phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4, respectively.

COLOUR AND PATTERN: Werner (1909) describes the type as "bright reddish-brown, with very obscure lighter dashes in longitudinal rows, flanks of anterior half of body with darker spots. Shields above the lips dark edged. Underneath yellowish, throat and chest sparsely dark flecked, chest with darker (more red-brown) median longitudinal lines". The holotype is now completely bleached, colour and pattern are unable to be distinguished. The more recent specimen (QM J37441), in alcohol has the dorsal surface brown with randomly scattered fine pale flecks, and a single row of pale spots laterodorsally from midway between level of ear and forelimb to regenerated basal portion of tail; head mottled light and dark. Pale dorsolateral stripe cream, extending from naris to rear of eye thence posteriorly along body and regenerated portion of tail, bordered below by fine black stripe which is most prominent anteriorly to a level just past forelimb, and which contacts its partner anteriorly across rostral. Lateral surface brown with fine dark and light flecks uppermost, becoming dark grey with irregular pale blotches on lower lateral surface approaching venter. Fore and hindlimbs mottled of light and dark brown. Venter pale white with scattered grey flecking on outer edges of throat.

Distribution and habitats. North-east coast of mainland New Caledonian and Isle of Pines (Fig. 46).

Caledoniscincus n. gen.

Type species. *Lygosoma austro-caledonica* Bavay, 1869: 21.

Diagnosis. *Caledoniscincus* is a member of the *Eugongylus* group of Greer (1979), it can be distinguished from all other genera in that group by the following combination of characters: frontoparietals fused; prefrontals moderate in size, usually well separated; supranasal or postnasal suture generally absent; lower eyelid with an obvious, centrally located semi-transparent disc; ear lobules moderately small; altantal arch fused to intercentrum; hemipenes deeply bifurcate; colour pattern features adult females retaining juvenile colouration but adult males changing tone and delineation of dorsal and lateral colouration.

Recognized species. *Caledoniscincus austrocaledonicus* (Bavay, 1869); *Caledoniscincus atropunctatus* (Roux, 1913); *Caledoniscincus festivus* (Roux, 1913); *Caledoniscincus orestes* n. sp.

Etymology. The name *Caledoniscincus* combines latin for Caledonia *(Caledonius)* with skink *(scincus)*. Species in the genus are largely confined to New Caledonia, and are widespread with one or more species occurring in most habitats.

Remarks. Species included in *Caledoniscincus* are moderately small to moderately large skinks very similar in overall morphology. All share the following characteristics of colouration and pattern: marked sexual dimorphism in adults with juveniles, subadults of both sexes and adult females similar in colour pattern; dorsal and lateral surfaces of adult females well delineated and in strong contrast, adult males distinctively coloured and patterned but with dorsal and lateral surfaces similar in colour and, unless defined by a pale laterodorsal stripe, tending to grade in colour and pattern rather than sharply delineated at dorsolateral edge.

All species of *Caledoniscincus* apart from *C. orestes* occur throughout most of mainland New Caledonia. *Caledoniscincus austrocaledonicus* and *C. atropunctatus* also occur in the Loyalty Islands, and *C. atropunctatus* also in Vanuatu.

Key to species of *Caledoniscincus*

1. Tail with distinct, dark, transversely aligned chevrons. 2

——Tail lacking dark chevrons; maximum SVL 53 mm. ..... *C. atropunctatus*

2. Dorsum with either vertebral or lateral pale striping or both. 3

——Dorsum without pale vertebral or lateral striping; large species, maximum SVL 66 mm. ..... *C. festivus*

3. Dorsum with pale vertebral stripe only; large species, maximum SVL 65mm; restricted to Mt Panie. ..... *C.* n. sp.

——Dorsum with either pale vertebral or lateral stripes, or both; maximum SVL 55 mm; widespread over most of New Caledonian mainland and Loyalty Islands. ..... *C. austrocaledonicus*

Caledoniscincus austrocaledonicus (Bavay)

Figs 49–55

Lygosoma austro-caledonica Bavay, 1869: 21.
Euprepes haplorhinus Günther, 1872: 419.
Lygosoma austro-caledonicum dorsovittatum Roux, 1913: 118.
Leiolopisma dorsovittatum bodoi Borner, 1980: 8.

Type material. NEOTYPE: *Lygosoma austro-caledonica* Bavay, AM R77757, here designated, adult female, SVL 54.5 mm (Figs 51, 52), 4 km from summit of Mt Aoupinie by road, New Caledonia, 21°11′S 165°16′E. Colour and pattern typical of adult females from northern and central populations, but with pale vertebral stripe faint but obvious. HOLOTYPE: *Euprepres haplorhinus* Günther, BM 1946.8.13.45, most

probably female, SVL 50.5 mm (Fig. 53), New Caledonia. Colour and pattern typical of adult females from northern and central populations. LECTOTYPE: *Lygosoma austrocaledonicum dorsovittatum* Roux, NHMB 7330, adult male, SVL 49.5 mm (Fig. 54), Heinghene, New Caledonia, 20°42′S 164°55′E. Colour and pattern typical of adult males from northern and central populations. NHMB registration tag reads "venter, sides and feet orange underneath".

Additional material examined. AM R77922, 77924-35, 77938, 77940-41, 77963-66, Berniers backyard at Poum, 20°14′S 164°02′E; AM R77971-80, 77982, Poum rubbish tip, 20°14′S 164°04′E; AM R77983-87, Poum, 20°14′S 165°02′E; AM R77905, 77908-14, 21 km north of Puebo on coast road, 20°17′S 164°26′E; NHMB 7251-54, 16870, 16884, 16898, 19071, 19078, Outbache, 20°26′S 164°38′E; AM R77900, beach below gendarmarie, Heinghene, 20°42′S 164°55′E; AM R77809-14, creek behind Kavatch forestry camp, 20°42′S 164°50′E; AM R77839, 14 km south of Heinghene River bridge, 20°43′S 165°05′E; NHMB 7326-27, 7261-62, 16075, 16855, 19081, Kone, 21°04′S 164°52′E; AM R77642-49, 77651-52, Mt Aoupinie forestry camp (500 m), 21°09′S 165°21′E; AM R77689-90, 77692, old campsite 2 km north-east of Mt Aoupinie forestry camp by road (500 m), 21°08′S 165°21′E; AM R77784-87, AM R77707, 77709-13, 77715-16, creek crossing 1 km north-east of Mt Aoupinie forestry camp by road (500 m), 21°08′S 165°21′E; AM R77735, 5 km north-east of Mt Aoupinie forestry camp by road, 21°07′S 165°22′E; AM R77737-41, 77744, 77755-56, summit of Mt Aoupinie (1086 m), 21°11′S 165°16′E; AM R77759-63, 6 km from summit of Mt Aoupinie by road, 21°11′S 165°16′E; AM R77601, 2 km north of Houailou airstrip, 21°14′S 165°37′E; AM R77545-59, Houailou airstrip,

Fig. 49. *Caledoniscincus austrocaledonicum* from Kuto, Isle of Pines.

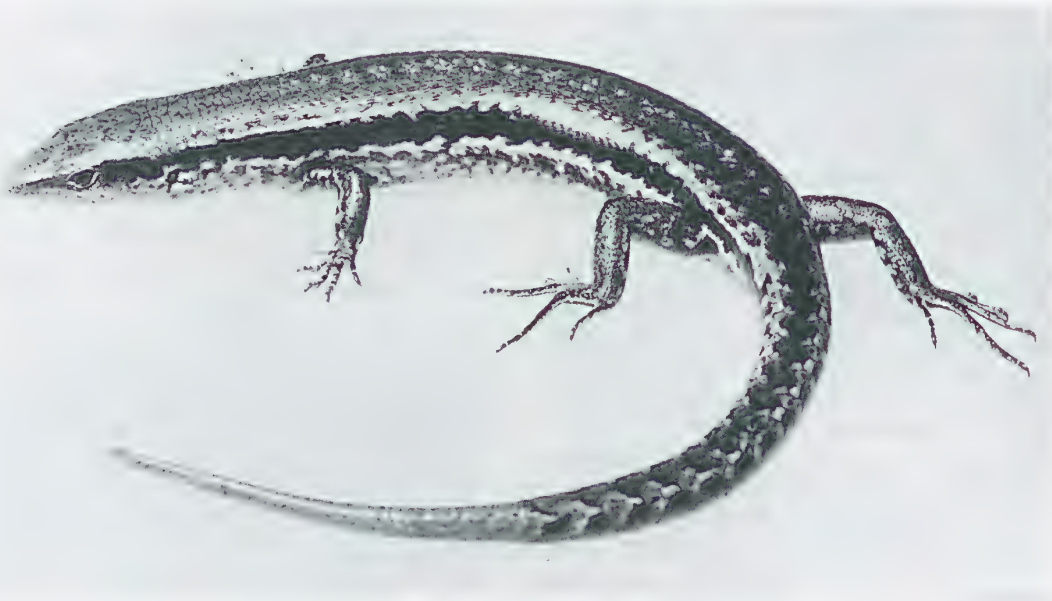


Fig. 50. *Caledoniscincus austrocaledonicum* from Heinghene.

21°16′S 165°37′E; AM R77529-31, 4 km north of junction of Poya Road, on Bourail - Houailou road, 21°29′S 165°28′E; AM R77521-23, La Font Poya, 9 km north-west of Moindu on Bourail road, 21°32′S 165°28′E; NHMB 7338, 7342, 7265-77, 16850, 17004, 18949, 19069, Mt Kanala (700 m), 21°35′S 165°56′E; QM J43992, Mt Rembai (700–900 m), 21°36′S 165°51′E; AM R78107-10, Uitoe near Tontouta, 22°05′S 166°08′E; AM R78237, 13 km west of Carenage turn off on Noumea to Yate road, 22°09′S 166°45′E; AM R78144, 4 km up the Mt Gouemba road, near Yate (300–350 m), 22°09′S 166°54′E; AM R78145, 77147, 78160, 78162, 78165-68, 78170-71, 78173-77, 78179, 78183, 78185-87, 78189, 78192-93, base of Mt Gouemba road, near Yate, 22°10′S 166°57′E; AM R78230, beach front 3 km south of La Fausse Yate bridge, 22°10′S 166°57′E; AM R78250-60, 2 km west of Plum turnoff on Mt Dore road, 22°17′S 166°37′E; AM R77407-10, 77414-18, 77420-21, 77428-45, 77448-53, Rue de Captain Ferraud, Fauboug Blanchot, Noumea, 22°18′S 166°27′E; AM R77401, 77403-06, 77456-59, 77461-63, 77465-71, 77473-75, 77477-80, 77482-84, 77486, 77488, 77490-94, 77496-504, Mt Coffyn, 22°18′S 166°27′E; AM R116047-48, Porc-Epic Island off Noumea, 22°19′S 166°36′E; AM R110289-93, Redika Island off Noumea, 22°31′S 166°37′E; QM J44002-03, Foret Thy Reserve (150 m).

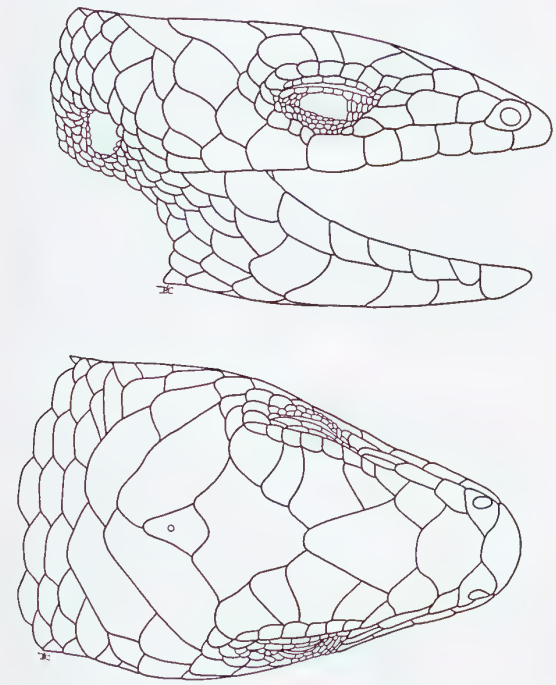


Fig. 51. Lateral and dorsal views of the head of AM R77757, neotype of *Lygosoma austrocaledonica* Bavay.

Loyalty Islands: NHMB 7296-99, 7357-58, 16854, Fayoue, Ouvea Island, 20°39′S 166°32′E; NHMB 7283-90, Kepenee, Lifou Island; NHMB 7291-92, 7354-56, 19079, Nathalo, Lifou Island, 20°47′S 167°16′E; NHMB 7272-78, 7347-49, 16883, 19070, 19077, 19083, Netche, Mare Island, 21°29′S 167°51′E.

Diagnosis. *Caledoniscincus austrocaledonicus* can be distinguished from all other species in the genus by the following combination of features in colouration and size: tail with distinctive, dark, transversely aligned chevrons; dorsum with either vertebral or lateral pale stripes, or both.

In size, *C. austrocaledonicus* (maximum SVL 55 mm) is similiar only to *Caledoniscincus atropunctatus* (maximum SVL 53 mm); *Caledoniscincus festivus* (maximum SVL 66.5 mm) and *Caledoniscincus orestes* (maximum SVL 65 mm) being much larger.

Description. The measurements and scalation for this description are based on 88 adult specimens from two northern localities in the vicinity of Poum (n = 26) and Mt Aoupinie (n = 37), and two southern localities in the

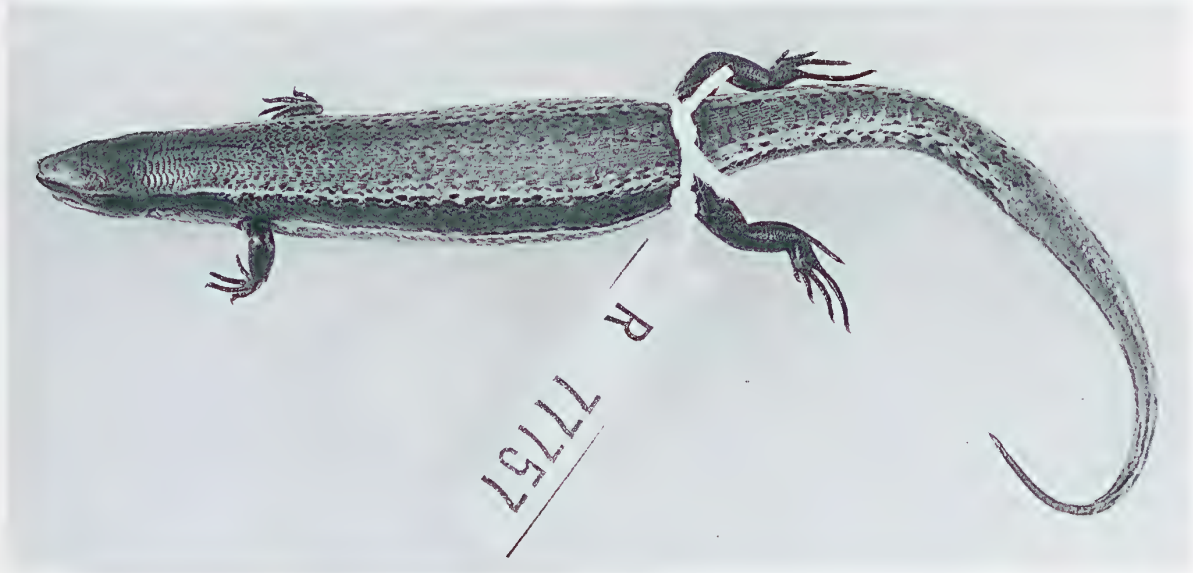


Fig. 52. AM R77757, neotype of *Lygosoma austrocaledonica* Bavay.

vicinity of Yate (n = 17) and Mt Dore (n = 8).

MEASUREMENTS: males begin to develop features of colouration distinct from adult females around a size 40 mm SVL (slightly larger in Mt Aoupinie highland sample at 43 mm SVL). The smallest apparently reproductively active females occur around a size of 37 mm SVL (again slightly larger in Mt Aoupinie highland sample at 45 mm SVL). Only males of 40 mm SVL and over, and females 37 mm SVL and over are included in the following body measurements.

Maximum size 55 mm SVL; distance from axilla to groin 54.1–62.8% of SVL ($\bar{x}$ = 58.7, n = 88); hindlimb length 32.7–44.2% of SVL ($\bar{x}$ = 39.3, n = 88); tail length ca. 126.4–188.1% of SVL ($\bar{x}$ = 155.4, n = 11).

SCALATION: frontonasal broader than long (sample from vicinity of Poum: W/L 112–140%, $\bar{x}$ = 127.9, n = 23); prefrontals moderate in size, widely separated; frontal near as broad as long (sample from vicinity of Poum: W/L 75–94.6%, $\bar{x}$ = 83.1, n = 23); frontoparietals fused; interparietal distinct; parietals each bordered by a single nuchal and upper secondary temporal scale; primary temporal single; upper and lower secondary temporals single; tertiary temporals 2.

Nasals moderately to widely separated, postnasal crease variably present (51.1% bothsides, 14.9% one side only, n = 47) or absent; 2 loreals in a horizontal sequence, anterior noticeably deeper than long, posterior longer than deep and shallower than anterior; anterior subocular usually 2 (85.6%, n = 88), anteriormost large and followed by a smaller scale, sometimes a single large scale; supraciliaries usually 7 (97.1%, n = 87); upper labials usually 7 (98.3%, n = 87) with fifth subocular and contacting lower eyelid; postlabials 2; lower labials usually 6 (96.5%, n = 87), first 2 contacting postmental; chinshields 3.

Lower eyelid with an obvious, centrally located semi-transparent disc, length 37.9–50% of total eye length (sample from vicinity of Poum: $\bar{x}$ = 44%, n = 24).

Ear opening with 2 (35.4%, n = 85)–3 (51%), rarely 1 or 4, enlarged auricular lobules anteriorly and numerous blunt conical scales around upper, lower and posterior edges.

Body scales of dorsal and lateral surfaces tricarinate, each keel usually interrupting posteriormost edge of scale, number of keels increasing towards nape; midbody scale rows 28–34 ($\bar{x}$ = 30.3, sd = 1.3, n = 88); paravertebral scales 56–68 ($\bar{x}$ = 61.3, sd = 2.3, n = 88).

Lamellae beneath fourth toe 23–33 ($\bar{x}$ = 27.6, sd = 1.9, n = 88).

OSTEOLOGY: premaxillary teeth 11 (90.9%, n = 11), or 10; maxillary teeth 19–26 ($\bar{x}$ = 23.8, sd = 2.7, n = 11); dentary teeth 23–32 ($\bar{x}$ = 28.7, sd = 2.7, n = 11); presacral vertebrae 29; phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4, respectively.

COLOUR AND PATTERN: *Caledoniscincus austrocaledonicus* is highly variable in colour pattern with distinct sexual dimorphism and geographic variation in patterns present. The most obvious difference between the sexes is clear demarkation between dorsal and lateral surfaces in adult females whereas in adult males these surfaces are similar in colour and tend towards a gradation in pattern unless clearly defined by a pale but rough-edged laterodorsal stripe.

Variation in both sexes in tone of dorsal colour, width and boldness of pale vertebral and laterodorsal stripes, and presence of pale midlateral stripe roughly aids in the recognition of two geographically distinct

Fig. 53. BM 1946.8.13.15, holotype of *Eurepes haplorhinus* Günther.

Fig. 54. NHMB 7330, lectotype of *Lygosoma austro-caledonicum dorsovittatum* Roux.

populations: one in the northern and central part of the main island (i.e. Poum, Koumac and Mt Aoupinie) and the other in the south (i.e. Yate and Mt Dore). Intermediate populations occur at Mt Kanala where males are typical of southern form and females a composite of northern-central and southern forms, and at Noumea where both northern-central and southern male and female forms occur. The pale midlateral stripe is the feature in which this pattern of geographic variation is most obvious.

a) Adult males. Dorsal surface mid to dark brown with pale flecks; distinct pale vertebral stripe grey-brown, rough-edged and variably defined, extending from nape to middle of body before breaking posteriorly into a series of poorly connected elongate blotches; head usually lighter than dorsum, with coppery flush and variably with a dark brown-black longitudinal streak on rostral (most common in southern form); pale laterodorsal stripe light grey-brown, rough-edged and variably defined, broad and distinct from lateral surface in northern and central populations, narrow and indistinct in southern populations. Lateral surface mid to dark brown, usually with pale midlateral stripe white and distinct. Tail mid to dark brown dorsomedially, broken into a series of interconnecting blotches; laterodorsal and upper lateral surface predominately grey-brown; remainder of lateral surface of tail mid to dark brown with chevrons of that colour intruding into lighter grey-brown upper surface. Venter (in life) cream anterior of forelimbs, generally orange, sometimes orange-yellow posteriorly.

b) Adult females. Dorsal surface light to mid brown, occasionally grey in northern and central populations, mid to dark brown in southern populations; pale vertebral stripe light brown to grey (lighter than adjacent dorsal), usually distinct, occasionally indistinguishable in individuals with light grey dorsal surface in northern populations (17% indistinct for Poum); pale laterodorsal stripe light brown to grey (same as vertebral stripe if present), broad with smooth dorsolateral edge distinct from lateral surface in northern and central populations, grey-brown and smooth edged but in poor

Fig. 55. Distribution of *Caledoniscincus austrocaledonicus* (closed circles) in New Caledonia.

contrast to dorsal and lateral surface in southern populations. Lateral surface mid to dark brown; pale midlateral stripe white, usually present in northern and central populations and defining a dark upper lateral from lighter lower lateral surface; rough and broken posteriorly in both sexes from Koumac; variably present in Kanala population occurring either poorly or prominently in some individuals; usually absent from southern populations, upper and lower lateral colouration a gradation. Tail as for adult males. Venter (in life) cream anterior to forelimbs, yellow-cream posteriorly, rarely bolder orange.

Distribution and habitats. *Caledoniscincus austrocaledonicus* is widely distributed over a variety of habitats on mainland New Caledonia (Fig. 55). It also occurs on a number of offshore islands including the Isle of Pines off the south-western corner of the main island (described as new subspecies *Leiolopisma dorsovittatum bodoi* by Börner 1980). Roux (1913) also recorded this species from all the Loyalty Islands. Reference to this species in a key to lizards of islands of New Hebrides is considered to be a mistake for *Caledoniscincus atropunctatus*.

Caledoniscincus austrocaledonicus inhabits low elevation open scrub and woodland (Fig. 1b,c), lowland and highland rainforest borders (Fig. 1e), and highland heath. In forest edge habitat, *C. austrocaledonicus* is syntopic with *Caledoniscincus festivus* and *C. atropunctatus*, the latter two species rarely being observed in more open habitat.

Reproduction. *Caledoniscincus austrocaledonicus* is oviparous, producing 1–5 eggs. Clutch size in high altitude areas (i.e. Mt Aoupinie range = 2–5, mode 3, n = 12) is greater than lowland locations (i.e. Noumea, Yate, Poum range = 1–4, mode 2, n = 27). Reproductively active females from the highlands are larger (SVL range 44.5–54.5, $\bar{x}$ = 50, n = 13) than those from the lowlands (SVL range 37–50, $\bar{x}$ = 42.5, n = 30).

Remarks. The description by Bavay (1869) recognizing two forms (Varieties A and B) of *Lygosoma austro-caledonica* indicates that the material was composite.

Boulenger (1887) redescribed *Lygosoma austro-caledonicum* Bavay, correctly placing *Euprepes haplorhinus* Günther in its synonomy.

Roux (1913) redescribed *Lygosoma austro-caledonicum* restricting it to Variety A (part) of Bavay, noting females greatly outnumbered males. Roux also described *Lygosoma austro-caledonicum dorsovittatum* n. subsp., and noted that this form also agreed in part with Bavay's Variety A, but that the material on which the description of this subspecies was based were mostly male.

Börner's (1980) recognition of *Lygosoma austro-caledonicum dorsovittatum* Roux as a full species by describing *Leiolopisma dorsovittatum bodoi* n. subsp. is unjustified as Roux's subspecies is based on males of *Lygosoma austro-caledonica* Bavay, 1869. Specimens descibed by Börner and those in the Australian Museum collection from the Isle of Pines fall within the range of variation observed for southern mainland and island populations of *Caledoniscincus austrocaledonicus*.

Caledoniscincus atropunctatus (Roux)

Figs 56–59

Lygosoma austro-caledonicum atropunctatum Roux 1913: 117.

Type material. LECTOTYPE: *Lygosoma austro-caledonicum atropunctatum*, NHMB 7308, adult male, SVL 49 mm (Figs 57, 58), Outbache, New Caledonia, 20°26′S 164°38′E.

Additional material examined. AM R77921, 77923, 77936, 77954, 77962, 77789-90, Poum, 20°14′S 164°02′E; NHMB 7603, Pam, 20°15′S 164°18′E; NHMB 7307, 7309-11, 19019, 19034, 19037, Outbache, 20°26′S 164°38′E; NHMB 7312, Toa, 20°33′S 164′48′E; AM R78069, Koumac Caves 9 km east of Koumac, 20°33′S 164°21′E; NHMB 7314, 19003, 19015, 19023, 19030, Kone, 21°04′S 164°52′E; AM R77732, 3 km north-east of Mt Aoupinie forestry camp by road (500 m), 21°07′S 165°22′E; AM R77573-94, Houailou airstrip, 21°16′S 165°37′E; AM R77524-28, 4 km north of junction of Poya road on Bourail to Houailou road, 21°29′S 165°28′E; NHMB 7315, Canala, 31°32′S 165°57′E; NHMB 7321, Negopo Tal, 21°32′S 165°54′E; NHMB 19029, Bourail, 21°34′S 165°29′E; NHMB 7316, 19028, Mt Kanala (700 m), 21°35′S 165°56′E; NHMB 7317, La Foa, 21°43′S 165°49′E; NHMB 7318-19, 19010, 19025, Ngoy Tal (200 m), 21°49′S 166°36′E; AM R116037-38, La Riviere Bleu, 22°06′S 166°40′E; AM R78229, beachfront 3 km south of La Fausse Yate bridge, 22°10′S 166°57′E; AM R78261-81, 2 km west of Plum turn off on Mt Dore road, 22°17′S 166°37′E; AM R77339-400, 77439, Noumea, 22°18′S 166°27′E.

Lifou Island, Loyalty Islands: NHMB 7324, 19014, Nathalo 20°47′S 167°16°E; NHMB 7324, Kepenee.

Diagnosis. *Caledoniscincus atropunctatus* can be distinguished from all other species in the genus by the following combination of colour features: tail with dorsal and lateral surfaces each more or less uniform i.e. without dark chevrons; dorsum with dorsal and lateral surfaces each more or less uniform, pale vertebral or lateral stripes lacking; snout uniform, dark midrostral streak always lacking.

In size, *C. atropunctatus* (maximum SVL 53 mm) is similiar only to *C. austrocaledonicus* (maximum SVL 55 mm), the species *C. festivus* (maximum SVL 66.5 mm) and *C. orestes* (maximum SVL 65 mm) being much larger.

Description. The measurements and scalation for this description are based on 39 adult specimens from the vicinity of Houailou (n = 19) and vicinity of Mt Dore (n = 20).

MEASUREMENTS: males begin to develop features of colouration distinct from adult females around a size 40 mm SVL. The smallest apparently reproductively active females occur around a size of 38 mm SVL. Only males 40 mm SVL and over, and females 38 mm SVL and over are included in the following body measurements.

Maximum SVL of 53 mm; distance from axilla to groin 50–61.6% of SVL ($\bar{x}$ = 57.3, n = 39); hindlimb

Fig. 56. *Caledoniscincus atropunctatus* from near Yate, New Caledonia.

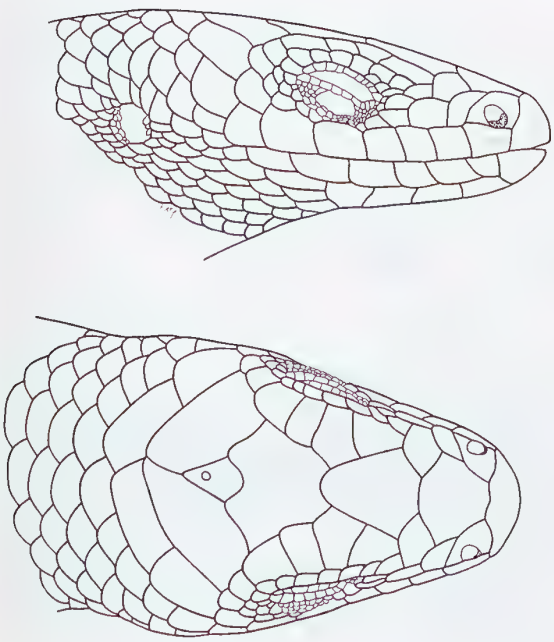


Fig. 57. Lateral and dorsal views of the head of NHMB 7308, lectotype of *Lygosoma austro-caledonicum atropunctatum* Roux.

length 30.2–39.2% of SVL ($\bar{x}$ = 34.1, n = 39) tail length ca. 142.5–151.3% of SVL ($\bar{x}$ = 149.8, n = 5).

SCALATION: frontonasal broader than long (W/L 142.9–188.9%, $\bar{x}$ = 161.5, n = 20); prefrontals moderate in size, widely separated; frontal near as broad as long (W/L 80.7–107%, $\bar{x}$ = 88.9, n = 20); frontoparietals fused; interparietal distinct; parietals each bordered by a single nuchal and upper secondary temporal scale; primary temporal single; upper and lower secondary temporals single, tertiary temporals 2.

Nasals moderately to widely separated, postnasal crease variably present (60% both sides, 15.4% 1 side only, n = 39), or absent; 2 loreals in a horizontal sequence, anterior noticeably deeper than long, posterior longer than deep and shallower than anterior; anterior suboculars usually only a single large scale (73.1%, n = 39), otherwise followed by 1–2 much smaller scales; supraciliaries usually 7 (97.4%, n = 39), rarely 8; upper labials 7, with fifth subocular and contacting lower eyelid; postlabials 2; lower labials usually 6 (94.9%, n = 39), rarely 5, first 2 contacting postmental; chinshields 3.

Lower eyelid with an obvious, centrally located semi-transparent disc, length 38.2–71.4 of total eye length ($\bar{x}$ = 48%, n = 20).

Ear opening with 2(42.3%, n = 37)–3(47.4%), rarely 4, enlarged auricular lobules anteriorly, and numerous blunt conical scales around upper, lower and posterior edges.

Body scales of dorsal and lateral surfaces tricarinate, each keel usually interrupting posteriormost edge of scale, number of keels increasing towards nape; midbody scale rows 28–32 ($\bar{x}$ = 29.6, sd = 0.9, n = 39); paravertebral scales 51–60 ($\bar{x}$ = 55.9, sd = 2.2, n = 39).

Lamellae beneath fourth toe 23–30 ($\bar{x}$ = 25.7, sd = 1.6, n = 39).

OSTEOLOGY: premaxillary teeth 11 (87.5%, n = 16), or 10; maxillary teeth 22–29 ($\bar{x}$ = 25.1, sd = 2, n = 16); dentary teeth 29–35 ($\bar{x}$ = 32.4, sd = 1.8, n = 16); presacral vertebrae 29 (87%, n = 23), rarely 30 (8.7%) or 28; postsacral vertebrae 49–51 (n = 2); phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4, respectively.

COLOUR AND PATTERN: there is marked sexual dimorphism in colour and pattern in adults of *Caledoniscincus atropunctatus*.

a) Adult males. Dorsal and lateral colour and pattern poorly demarcated. Dorsal surface of body and tail dark brown with numerous fine light cream flecks; head

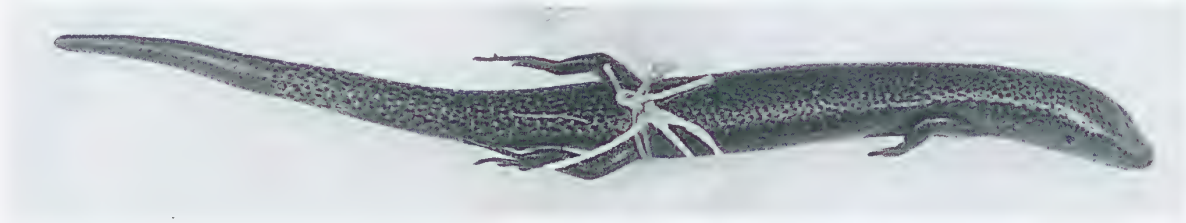


Fig. 58. NHMB 7308, lectotype of *Lygosoma austro-caledonicum atropunctatum* Roux.

Fig. 59. Distribution of *Caledoniscincus atropunctatus* (closed circles), *Caledoniscincus festivus* (open star), both *C. festivus* and *C. atropunctatus* from same locality (open star in closed circle), and *Caledoniscincus orestes* n. sp. (open circle) in New Caledonia.

brown with dark brown-black spots and overall coppery tinge, dark midrostral streak absent. Pale dorsolateral stripe extending from posterior corner of eye to just past forelimbs, upper edge obscure, lower edge distinct and contrasting with darker lateral surface. Lateral surface dark brown with a coppery tinge anterior to forelimbs in some specimens, and with sparse light flecking anteriorly and dorsolaterally; colour of lateral surface tending to be lighter ventrolaterally, but some specimens retaining dark tone throughout the body depth. Tail a continuation of dorsal and lateral colour and pattern, lacking dark dorsal or lateral chevrons characteristic of other *Caledoniscincus*. Fore and hindlimbs with similar dorsal and lateral colour and differentiation as dorsum.

b) Adult females. Dorsal surface mid brown with fine dark flecking either uniformly scattered or restricted to middorsum; nape and head with copperish suffusion; rostral lacking dark midrostral streak. Pale dorsolateral stripe faint, light brown, only present anteriorly. Lateral surface dark charchoal-black, more or less uniform in intensity but tending to become lighter ventrolaterally. Tail similar in colour and pattern to the dorsal and lateral surfaces, no dark chevrons present. Fore and hindlimbs dark overall.

c) Subadults and juveniles. Subadult males and females (30–37 mm SVL) indistinguishable, both sexes having the female colour pattern. Smallest readily distinguished specimen with adult male pattern 40 mm SVL. Juvenile pattern slightly different to subadult, uniform light brown on dorsal surface, and lacking dark flecking or copper tinge anteriorly.

d) Colour in Life. Unlike other *Caledoniscincus,* adult *C. atropunctatus* lack ventral colouration of orange, yellow or pink, tending to be dirty cream to white.

Distribution and habitats. *Caledoniscincus atropunctatus* is distributed over most of mainland New Caledonia. It is also recorded from Lifou Island in the Loyalty Islands group and Vanuatu.

Caledoniscincus atropunctatus is most common in dense lowland forest but also inhabits coastal scrub (Fig. 1a,b) and mid altitude rainforest on Mt Kanala (700 m) and on Mt Aoupinie (ca. 400 m) (Fig. 1f). At lowland forest edge habitat *C. atropunctatus* is syntopic with both *C. austrocaledonicus* and *C. festivus*. Within forested lowland gullies *C. atropunctatus* and *C. festivus* are syntopic whereas *C. austrocaledonicus* rarely enters closed forest, prefering more open habitat.

Reproduction. *Caledoniscincus atropunctatus* is oviparous with clutch size of 2–3 eggs. The smallest specimen with shelled oviducal eggs was 40 mm SVL while the smallest specimen with enlarged yolked ovarian follicles was 38.5 mm SVL.

Remarks. Roux's (1913) *Lygosoma austrocaledonicum atropunctatum* n. subsp. was based on Bavay's (1869) 'Variety B' of *Lygosoma austrocaledonica.*

Caledoniscincus festivus (Roux)
Figs 59–63

Lygosoma austro-caledonicum intermedium Roux 1913: 119.
Lygosoma austro-caledonicum festivum Roux 1913: 120.

Type material. LECTOTYPES: *Lygosoma austrocaledonicum festivum* Roux, NHMB 7366, adult female, SVL 59.5 mm (Figs 61, 62), Canala, New Caledonia, 21°32′S 165°57′E. *Lygosoma austro-caledonicum intermedium* Roux, NHMB 7362, adult male, SVL 61 mm (Fig. 63), Ciu (300 m), New Caledonia, 21°34′S 165°58′E.

Additional material examined. AMR 77840, 14 km south of Heinghene River Bridge, 20°43′S 165°05′E; NHMB 7363-64, Kone, 21°04′S 164°52′E; AM R77676, Mt Aoupinie forestry camp (500 m), 21°09′S 165°20′E; NHMB 7368, Nio (300 m), 21°20′S 165°43′E; NHMB 7359-60, Canala, 21°32′S 165°57′E; NHMB 7367, Ciu (300 m), 21°34′S 165°58′E; NHMB 7365, La Foa (100 m), 21°43′S 165°49′E; NHMB 7371-73, Ngoy Tal, 21°49′S 166°36′E; AM R116036, La Riviere Bleu, 22°06′S 166°40′E; NHMB 7375-76, Yate, 22°09′S 166°54′E; AM R78214-15, 78217-18, base of Mt Gouemba road, near Yate, 22°10′S 166°57′E; AM R78239-44, 78346-47, 2 km west of Plum turnoff on Mt Dore road, 22°17′S 166°37′E; NHMB 7361, 7369-70, Corinde.

Diagnosis. *Caledoniscincus festivus* can be distinguished from all other species in the genus by the following combination of colour features: tail with a row of distinctive dark chevrons; dorsal and lateral surfaces each more or less uniform, pale vertebral or lateral stripes lacking; snout with dark vertical midrostral streak.

In size, *C. festivus* (maximum SVL 66.5 mm) is approached only by *C. orestes* (maximum SVL 65 mm), the species *C. austrocaledonicus* (maximum SVL 55 mm) and *C. atropunctatus* (maximum SVL 53 mm) being much smaller.

Fig. 60. *Caledoniscincus festivus* male **(a)** from Mt Aoupinie Forestry camp (500 m) and *C. festivus* female **(b)** from La Riviere Bleu.

Description. This description is based on 26 adult (including types), one subadult and four juvenile specimens.

MEASUREMENTS: males begin to develop features of colouration distinct from adult females at 61 mm SVL (smallest adult male). The smallest apparently reproductively active female was 56 mm SVL. Only males 61 mm SVL and over, and females 56 mm SVL and over are included in the body measurements.

Maximum SVL 66.5 mm; distance from axilla to groin 53.8–62.2% of SVL ($\bar{x}$ = 58.7, n = 26); hindlimb length 35–41.8% of SVL ($\bar{x}$ = 37.4, n = 26); tail length ca. 142.6–180.3% of SVL ($\bar{x}$ = 160.3, n = 4).

SCALATION: frontonasal broader than long (W/L 139.6–158.5%, $\bar{x}$ = 148.1, n = 10); prefrontals moderate in size, widely separated; frontal near as broad as long (W/L 82.5–93.3%, $\bar{x}$ = 88, n = 10); frontoparietals fused; interparietals distinct; parietals each bordered by a single nuchal and upper secondary temporal scale; primary temporal single; upper and lower secondary temporals single; tertiary temporals 2.

Nasals moderately to widely separated, postnasal crease variably present (33% both sides, 22.3% one side only, n = 27), or absent; 2 loreals in a horizontal sequence, anterior noticeably deeper than long, posterior longer than deep and shallower than anterior; anterior suboculars usually 2 (84%, n = 31), anteriormost large and followed by a smaller scale, sometimes a single large scale; supraciliaries 7; upper labials 7, with fifth subocular and contacting lower eyelid; postlabials 2; lower labials 6, first 2 contacting postmental; chinshields 3.

Lower eyelid with an obvious, centrally located semi-transparent disc, length 36.6–55% of total eye length ($\bar{x}$ = 44.2%, n = 28).

Ear opening with 2(60%, n = 25)–3(32%), rarely 4, enlarged auricular lobules anteriorly, and numerous blunt conical scales around upper, lower and posterior edges.

Body scales of dorsal and lateral surfaces tricarinate, each keel usually interrupting posteriormost edge of scale in males, weaker in females, number of keels increasing towards nape; midbody scale rows 32–34 ($\bar{x}$ = 32.9, sd = 1, n = 31); paravertebral scales 60–66 ($\bar{x}$ = 61.9, sd = 1.3, n = 31).

Lamellae beneath fourth toe 24–31 ($\bar{x}$ = 26.5, sd = 1.4, n = 29).

OSTEOLOGY: premaxillary teeth 11 (87.5%, n = 8) or 12; maxillary teeth 17–23 ($\bar{x}$ = 19.3, sd = 1.7, n = 8); dentary teeth 20–26 ($\bar{x}$ = 23.6, sd = 2, n = 8); presacral vetebrae usually 29 (90%, n = 10), rarely 28; phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4, respectively.

COLOUR AND PATTERN: there is marked sexual dimorphism in colour and pattern between adults of *Caledoniscincus festivus*. The most obvious differences are: clear demarcation between dorsal and lateral surfaces in females vs a graduation in colour in males; monochromatic dorsal and lateral colouration in

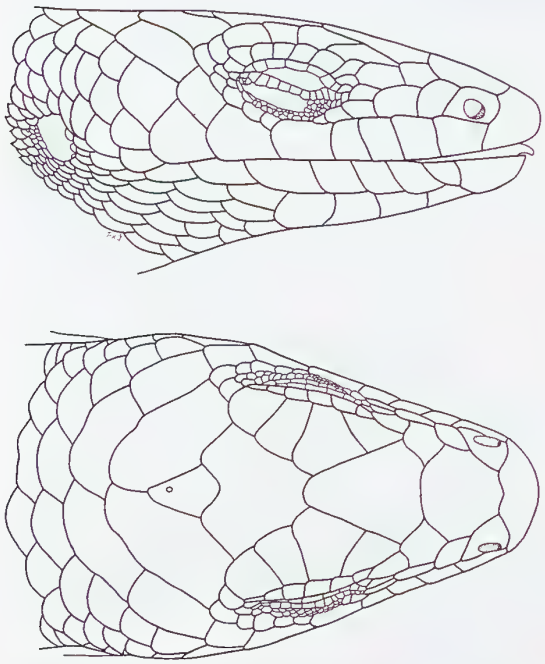


Fig. 61. Lateral and dorsal views of the head of NHMB 7366, lectotype of *Lygosoma austro-caledonicum festivum* Roux.

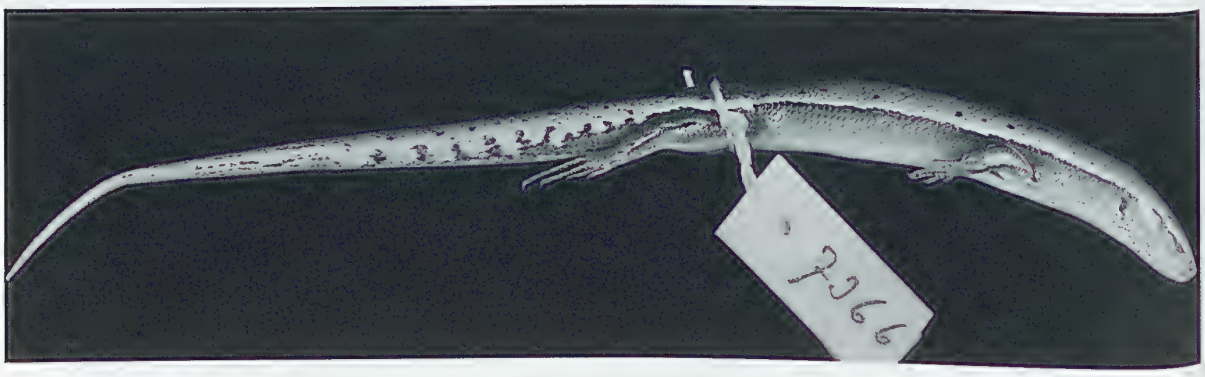


Fig. 62. NHMB 7366, lectotype of *Lygosoma austro-caledonicum festivum* Roux.

females vs polychromatic colouration in males.

a) Adult males. Dorsal surface mid brown with fine white flecks; light laterodorsal stripe, grey, continuing onto tail; head mid brown, rostral usually with a prominent black, vertical streak. Delineation of dorsal and lateral surfaces rough-edged but obvious. Lateral surface a gradation from dark to lighter brown approaching venter, and with irregular white flecks most prominent in region of forelimb; side of head dark brown with numerous pale flecks, distinct from uniform mid brown dorsal colour. Tail mid brown dorsomedially; laterodorsal and upper lateral surface predominately grey; remainder of lateral surface mid brown with chevrons of that colour intruding into lighter grey upper surface. Venter cream, lateral throat and chin shields with fine black flecks. Fore and hindlimbs with similar colour and demarcation as body.

b) Adult females. Dorsal surface uniform mid brown to light grey, usually with fine, longitudinally aligned dark flecks on laterodorsal surface; head similar. Pale narrow dorsolateral line extending from naris to just past hindlimbs. Lateral surface a gradation from dark smokey black uppermost to dark grey approaching the venter. Tail similar to adult males but with dorsal and laterodorsal colours sometimes indistinct, and dark lateral chevrons less pronounced. Fore and hindlimbs similar in colouration and demarcation to body. Otherwise as for adult males.

c) Subadults. Typical adult female colour pattern (single male SVL 39 mm).

d) Juveniles (series of four from Mt Dore and Mt Gouemba). Dorsal surface light grey with brown tinge to posterior half of body. Lateral surface uniform dark brown delineated from dorsal surface by fine black line extending from naris to just past level of hindlimbs, fading on tail; side of head lighter than rest of lateral surface. Venter pale with some dark flecking on throat and chest scales.

Juvenile *C. festivum* are readily distinguished from juveniles of other *Caledoniscincus* species by their larger size, more robust appearance, sharply contrasting uniform dark lateral and lighter dorsal colouration, and prominent dark midrostral streak.

e) Colour in Life. Adult male and female individuals from Mt Dore with a yellow flush to venter from level of forelimb to end of tail, anterior to forelimbs pinkish with fine dark flecking.

Distribution and habitats. *Caledoniscincus festivus* is recorded from the mid and southern east coast and highlands, and sporadically on the west coast (Fig. 59) of the New Caledonian mainland. It has not been recorded from the far north of the main island (as was noted by Roux).

Caledoniscincus festivus inhabits densely forested lowland gullys, cleared edges of lowland rainforest, and highland rainforest edge habitat (Mt Aoupine 500 m, Fig. 1f). Individuals were generally observed at the edge of the forest (syntopically with *C. austrocaledonicus* and *C. atropunctatus* in the lowlands and with *C. austrocaledonicus* in the highlands) or in small sunlit patches on the forest floor.

Reproduction. *Caledoniscincus festivus* is oviparous with a clutch size of 4–6. Shelled oviducal eggs were found in specimens in Roux's collection made in August 1911, and enlarged ovarian eggs in our collection made in December 1978.

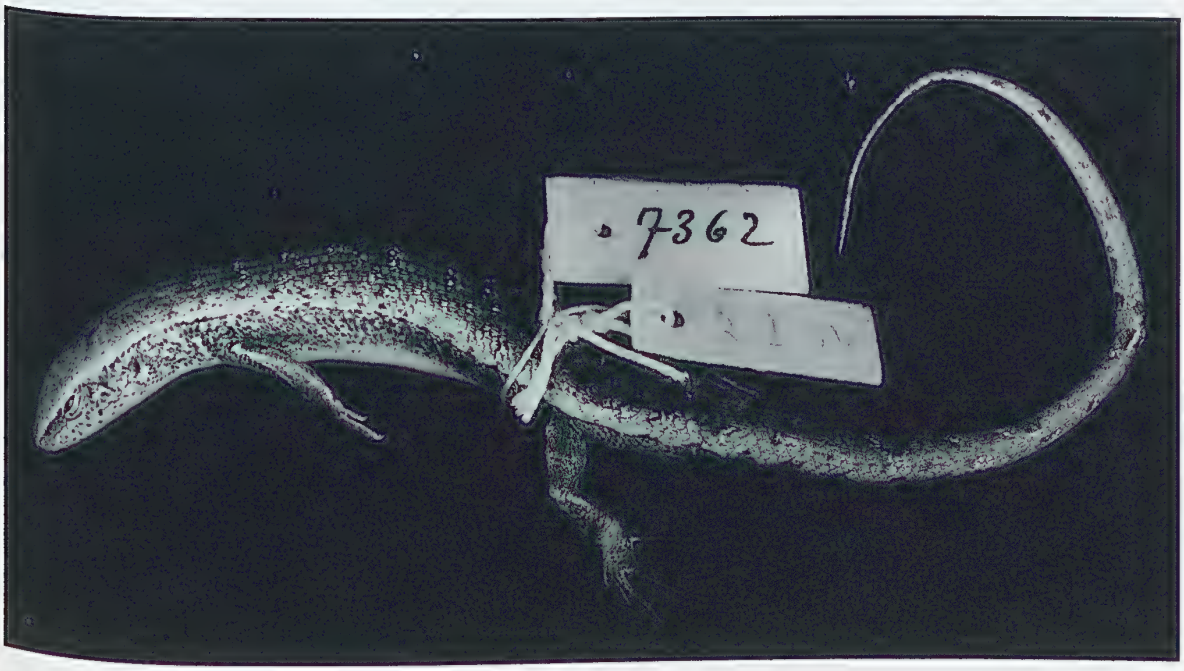


Fig. 63. NHMB 7362, lectotype of *Lygosoma austro-caledonicum intermedium* Roux.

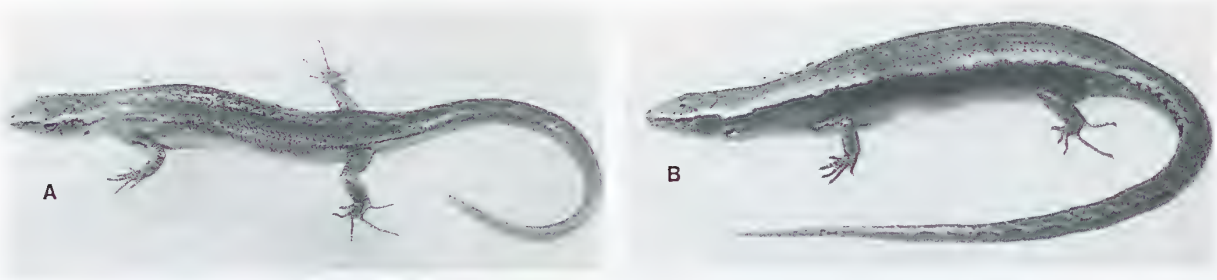


Fig. 64. *Caledoniscincus orestes* n. sp. male **(a)** and female **(b)** from near the summit of Mt Panie (1400 m), New Caledonia.

Caledoniscincus orestes n. sp.

Figs 60, 64–67

Type Material. HOLOTYPE: AM R77882, adult male, SVL 60 mm, Mt Panie (c.a. 900–930 m), New Caledonia, 20°33′S 164°45′S, collected by R. Sadlier & P. Rankin, 17 Dec 1978 (Figs 65, 66). PARATYPES: All specimens collected from Mt Panie: AM R77878 (760 m); AM R77881, 77883 (900–930 m); AM R77879, 77884-87 (1400 m); NHMB 7343-44 (500 m).

Diagnosis. *Caledoniscincus orestes* can be distinguished from all other species in the genus by the following combination of features in colour and size: tail with distinctive dark chevrons; dorsum with pale vertebral stripe; snout with dark midrostral streak.

In size, *C. orestes* (maximum SVL 65 mm) is approached only by *C. festivus* (maximum SVL 66.5 mm): the species *C. austrocaledonicus* (maximum SVL 55 mm) and *C. atropunctatus* (maximum SVL 53 mm) being much smaller.

Etymology. *Orestes* is the Latin word for mountain climber and alludes to the high altitudes inhabited by the species.

Description. This description is based on eight adult, two subadult and two juvenile specimens from Mt Aoupinie.

MEASUREMENTS: males begin to develop features of colouration distinct from adult females around a size of 55 mm SVL. Only individuals of 55 mm SVL and over are included in the following body measurement.

Maximum SVL 65 mm; distance from axilla to groin 58.6–64.9% of SVL ($\bar{x}$ = 60.2, n = 8); hindlimb length, 30.9–37.6% of SVL ($\bar{x}$ = 34.7, n = 8); tail length ca. 130.8–135% of SVL ($\bar{x}$ = 132.3, n = 3).

SCALATION: frontonasal broader than long (W/L 137.8–169.4%, $\bar{x}$ = 153.6, n = 8); prefrontals moderate in size, widely separated; frontal near as broad as long (W/L 78.6–91.7%, $\bar{x}$ = 85.4, n = 8); frontoparietals fused; interparietal distinct; parietals each bordered by a single nuchal and upper secondary temporal scale; primary temporal single; upper and lower secondary temporals single; tertiary temporals 2.

Nasals moderately to widely separated, postnasal crease variably present; 2 loreals in a horizontal sequence, anterior noticeably deeper than long, posterior longer than deep and shallower than anterior; anterior suboculars usually 2 (85%, n = 10), anteriormost large and followed by a smaller scale, occasionally followed by 2 smaller scales or present as a single large scale; supraciliaries 7; upper labials 7, with fifth subocular and contacting lower eyelid; postlabials 2; lower labials 6, first 2 contacting postmental; chinshields 3.

Lower eyelid with obvious, centrally located semi-transparent disc, length 44–51.2% of total eye length ($\bar{x}$ = 46.5, n = 7).

Ear opening with usually 3 (83.3%, n = 9), occasionally 2 or 4, enlarged auricular lobules anteriorly, and numerous blunt conical scales around upper, lower and posterior edges.

Body scales of dorsal and lateral surfaces tricarinate, each keel usually interrupting posteriormost edge in

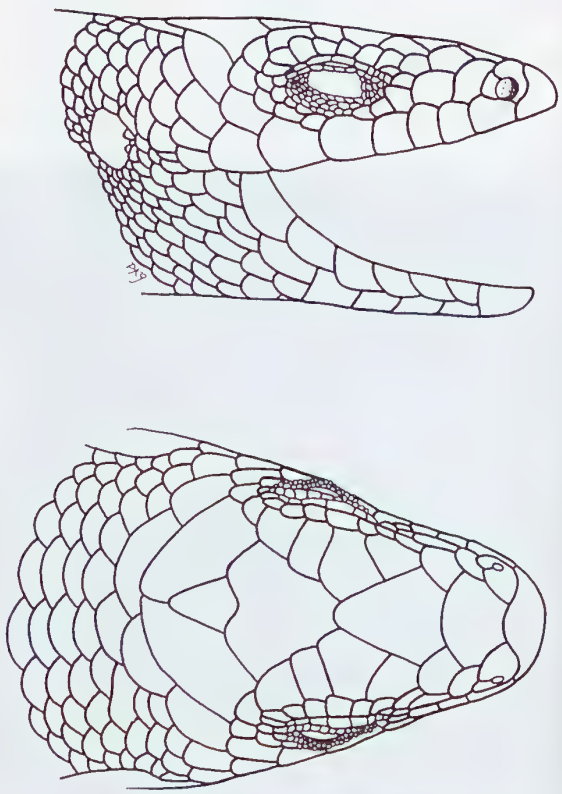


Fig. 65. Lateral and dorsal views of the head of AM R77882, holotype of *Caledoniscincus orestes* n. sp.

males, weaker in females, number of keels increasing towards nape; midbody scale rows 32–34 ($\bar{x}$ = 32.9, sd = 0.9, n = 12); paravertebral scales 56–63 ($\bar{x}$ = 58.7, sd = 1.9, n = 12).

Lamellae beneath fourth toe 24–28 ($\bar{x}$ = 25.2, sd = 1.3, n = 12).

OSTEOLOGY: premaxillary teeth 11 (50%, n = 6), 12 (16.7%) or 13; maxillary teeth 25–31 ($\bar{x}$ = 27.6, sd = 1.9, n = 5); dentary teeth 33–38 ($\bar{x}$ = 35.1, sd = 1.7 n = 5); presacral vertebrae 29 (50%, n = 6) or 30; phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4, respectively.

COLOUR AND PATTERN: adults of both sexes similar in colour on dorsal surface; marked sexual dimorphism occurs in intensity of colour distinguishing dorsal and lateral surfaces.

a) Adult males. Dorsal surface dark brown with scattered light flecks; vertebral stripe light brown to grey, prominent over most its length from nape to just past hindlimbs, sometimes broken into series of more or less elongate blotches; head and nape lighter with coppery flush, continuous laterally onto face and side of neck anterior to forelimb; midrostral streak of snout dark and prominent with broad lower edge. Dorsolateral

Fig. 66. AM R77882, holotype of *Caledoniscincus orestes* n. sp.

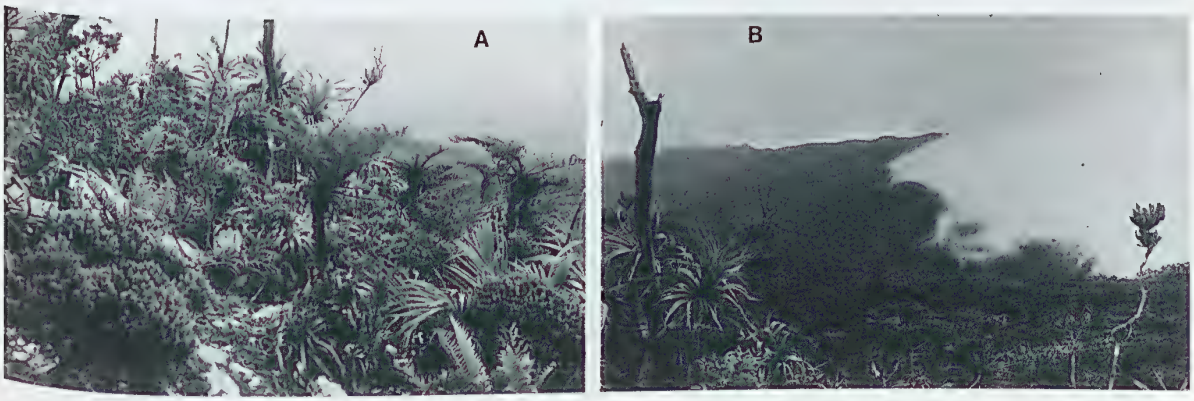


Fig. 67. High altitude rainforest (1400 m) on Mt Panie showing **(a)** the quartz outcrop at the type locality of *Caledoniscincus orestes*, and **(b)** the surrounding, mist-enshrouded ridges at this elevation.

stripe fine, black, extending posteriorly from rostral to just past hindlimbs, prominent anteriorly and sharply contrasting with lighter brown dorsal and lateral surface. Lateral surface mid to light brown becoming pale brown ventrolaterally; contrast between dorsal and lateral surfaces less marked than in females. Tail mid to dark brown dorsomedially, usually present as a series of large broadly contacting chevrons; laterodorsal and upper lateral surface predominately light grey; remainder of tail mid to dark brown with fine dark chevrons intruding onto lighter grey upper surface. Fore and hindlimbs with colour and demarcation of pattern similar to dorsal and lateral surfaces of body.

b) Adult females. Dorsal surface similar to adult males. Lateral surface uniform smokey black with a faint coppery flush anterior to forelimbs, sharply contrasting with dorsal surface. Fine black dorsolateral line (as described for males) obscured over most its length by dark lateral colour.

c) Subadult. Similar to adult females, but pale vertebral stripe indistinct (AM R77881).

d) Juveniles. Similar to adult females but more lightly coloured dorsally (mid to light brown) with no obvious pale vertebral stripe (AM R77886-7).

Change from juvenile to adult colouration apparently accomplished by overall darkening of dorsum except along vertebral line.

e) Colour in Life. Adults with yellow ventral flush from level of forelimbs posteriorly to end of tail; anterior of forelimbs russet and continuing over face. Subadult with dull pinkish flush to throat, remainder of venter yellow.

Iris dark, but still noticeably lighter than pupil.

Distribution and habitat. All AM specimens of *Caledoniscincus orestes* were collected along the track to the summit of Mt Panie (Fig. 59) in the north-east of mainland New Caledonia. Most were from the vicinity of a small quartz outcrop at 1400 m (Fig. 67), on an exposed ridge with a vegetation cover of very low heath. Other individuals were observed basking alongside the track at lower altitudes and samples were collected at 900–930 and 760 m. The habitat at lower altitudes was a low, dense, single story of palms, broadleafs, pandanus and ferns.

The two paratypes (NHMB 7243-4) collected by Roux & Sarasin in 1913 were recorded as coming from 500 m on Mt Panie.

Reproduction. Two gravid females of 61 and 65 mm SVL collected 17 December 1978 contained 5 (2/3) and 8 (4/4) shelled oviducal eggs respectively.

Sigaloseps n. gen.

Type species. *Lygosoma deplanchei* Bavay, 1869:

Diagnosis. *Sigaloseps* is a member of the *Eugongylus* group of Greer (1974), it can be distinguished from all other genera in that group by the following combination of characters: frontoparietals fused; supranasals and or postnasal sutures absent; ear lobules very small, blunt and rounded, recessed below edge of surrounding body scales; atlantal arches fused to intercentrum; body scales smooth.

Recognized species. *Sigaloseps deplanchei* (Bavay, 1869).

Etymology. The name *Sigaloseps* combines the Greek for glossy or shiny *(sigaloeis)* with that for lizard *(seps)*. The sole species in the genus is smooth-scaled and apparently restricted to the serpentine area of southern New Caledonia. The generic name *Sigaloseps* alludes to both the smooth body scales of this skink and shiny glossy nature of the mica rich rock type that is termed 'serpentine'.

Sigaloseps deplanchei (Bavay)
Figs 68–71

Lygosoma deplanchei Bavay, 1869: 23.
Hinulia tetragonurus Günther, 1872: 420.

Type material. LECTOTYPE: *Lygosoma deplanchei* Bavay, BM 86.9.16.1, here designated, sex indeterminate, SVL 42 mm (Fig. 69), 1 of 2 original syntypes BM 86.9.16.1-2 from New Caledonia. HOLOTYPE: *Hinulia tetragonurus* Günther, BM 71.4.16.42, male, SVL 44 mm (Fig. 70), recorded from "Feejee Islands" in type description (Günther 1892), later ammended to "New Caledonia" in BM catalogue.

Additional material examined. NHMB 7195-97, Ngoi Tal, 21°49′S 166°36′E; NHMB 7198-7201, 7205-06, AM R6672, Yate, 22°09′S 166°54′E; QM J43994-95, Mt Koghis, 22°10′S 162°32′E; AM R78246-7, 2 km west of Plum turnoff on Mt Dore road, 22°17′S 166°37′E.

Diagnosis. Species diagnosis same as for genus.

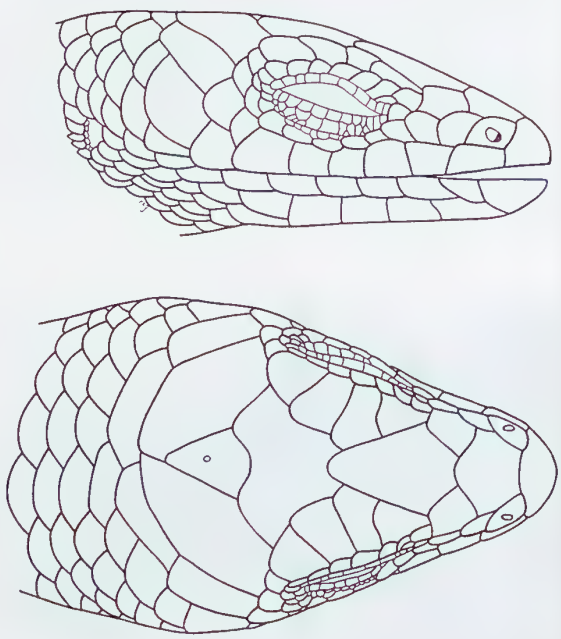


Fig. 68. Lateral and dorsal views of the head of NHMB 7195, a specimen of *Sigaloseps deplanchei* (Bavay).

Description. This description is based on 14 adult (including lectotype of *L. deplanchei* Bavay and holotype of *H. tertragonurus* Günther) and two subadult specimens.

MEASUREMENTS: Only adults 36 mm SVL and over are included in the body measurements. Maximum SVL of 44 mm; distance from axilla to groin 50.6–59.2% of SVL ($\bar{x}$ = 55.2, n = 16); hindlimb length 29.5–36% of SVL ($\bar{x}$ = 32.3, n = 16); tail length 120% of SVL (n = 2).

SCALATION: frontonasal broader than long (W/L 112–136%, $\bar{x}$ = 125.6, n = 10); prefrontals large, moderately to widely separated; frontoparietals fused; interparietal distinct; parietals each bordered by a single nuchal and upper secondary temporal scale; primary temporal single; upper and lower secondary temporals single; tertiary temporals 2.

Nasals widely separated; 2 loreals in a horizontal sequence; supraciliaries usually 7 (87.5%, n = 16), rarely 6; upper labials usually 7 (96.9%, n = 16), rarely 6, with fifth or fourth subocular respectively, separated from lower eyelid by a complete subocular scale row; postlabials 2; lower labials 6, first 2 contacting postmental; chinshields 3 each side, first pair in broad contact.

Lower eyelid variably scaly or with centrally located, undivided semi-translucent window. Most specimens from Ngoy Tal on the east coast of New Caledonia with lower eyelid fragmented by sutures dividing it into a number of opaque scales, largest located centrally, and becoming progressively smaller peripherally. Single specimen from Ngoy Tal and all but one from Yate (also on the east coast) with a more obvious opaque window in lower eyelid divided by one or more longitudinal sutures and surrounded by smaller granular shaped scales (condition for types BM 86.9.16.1 and BM 71.4.16.42). Single specimen from Yate lacking longitudinal sutures, and appearing more as a moderately large centrally located opaque disc. Specimens from Mt Dore and Mt Koghis on the west coast usually (80%, n = 5) with an obvious centrally located semi-transparent disc 30% of eye length, less frequently divided anteriorly or posteriorly by one or more longitundinal sutures.

Ear opening with 2 (64.5%, n = 16), 3 (22.6%), rarely 4 small, acute anterior lobules, and a number of small rounded lobules on posterior and lower edges.

Body scales smooth; midbody scale rows 24–28 ($\bar{x}$ = 26.5, sd = 1.1, n = 16); paravertebral scales 47–58 ($\bar{x}$ = 51, sd, 2.6, n = 16).

Lamellae beneath fourth toe 22–27 ($\bar{x}$ = 24.7, sd = 1.4, n = 15).

OSTEOLOGY: premaxillary teeth 10(50%, n = 2)–11; maxillary teeth 24–25 (n = 2); dentary teeth 25–28 (n = 2); presacral vertebrae 29 (n = 9); postsacral

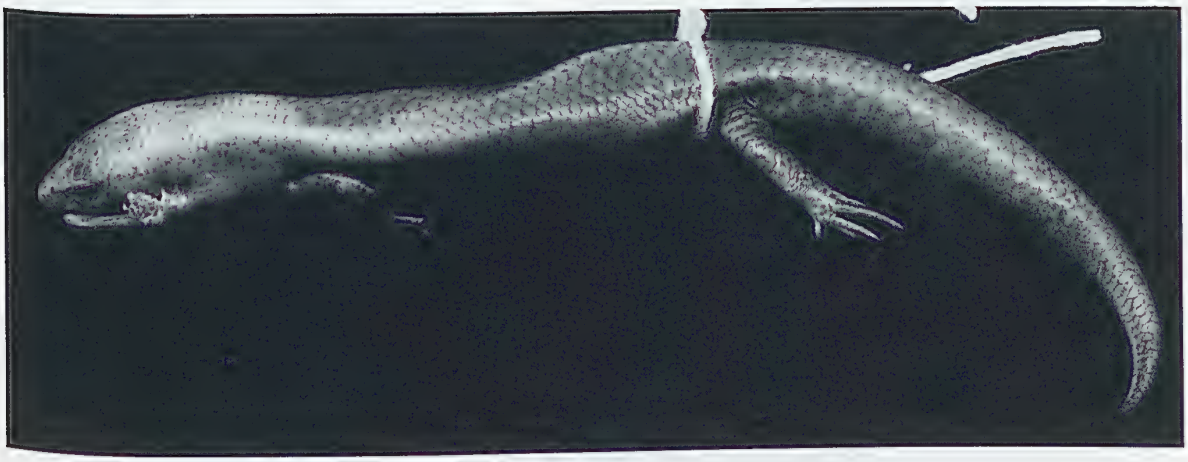


Fig. 69. BM 86.9.16.1, lectotype of *Lygosoma deplanchei* Bavay.

Fig. 70. BM 71.4.16.42, holotype of *Hinulia tetragonurus* Günther.

vertebrae 37 (n = 1); phalangeal formula for manus and pes 2.3.4.5.3. and 2.3.4.5.4, respectively.

COLOUR AND PATTERN: dorsal surface mid to dark brown, occasionally (east coast specimens) with scattered darker flecks longitudinally aligned to give 2 parallel vertebral lines. Lateral surface light to mid brown (paler than dorsal surface) between fore and hind limbs, with (east coast specimens) or without (west coast) numerous dark flecks uppermost; anterior to forelimb tan with dark flecking over side of head (east coast) or with dark flecks uppermost (appearing darker than dorsal surface and varying in intensity), including a dark streak facially from nare to anterior corner of eye; upper and lower labials each with a dark median streak (west coast specimens). Limbs as for dorsum but with numerous fine dark flecks. Venter dull white, in life (2 specimens from Mt Dore on west coast) orange from level of forelimbs to level of tail, yellowish below tail, anterior to forelimbs reddish orange to pinkish flush. Iris pale brown.

Distribution and habitats. Roux noted this species has only been recorded from the serpentine area in the south of mainland New Caledonia and never from the northern part of the island. This observation is here supported (Fig. 71). Roux's material was collected on the east coast at Valle Ngoi (200 m) and in the vicinity of Yate. Recent material has been collected in lowland rainforest on the west coast at Mt Dore and Mt Koghis.

The two individuals of *S. deplanchei* observed at Mt Dore were active at mid morning on the surface of thick leaf litter overlying a labyrinth of broken rock, but appeared reluctant to enter direct sunlight.

Remarks. Bavay's (1869) description of *Lygosoma deplanchei* lists measurements of a singe specimen, but two syntypes (BM 86.9.16.1-2) exist and Bavay refers also to having encountered this species in at least three different habitats.

For this species, Bavay described a lower eyelid with a transparent disc. In the BM syntypes the lower eyelid is scaled. However, Bavay also described a transparent disc in the lower eyelid for *Anotis mariei* Bavay and *Lygosoma gracilis* Bavay, but these are here regarded

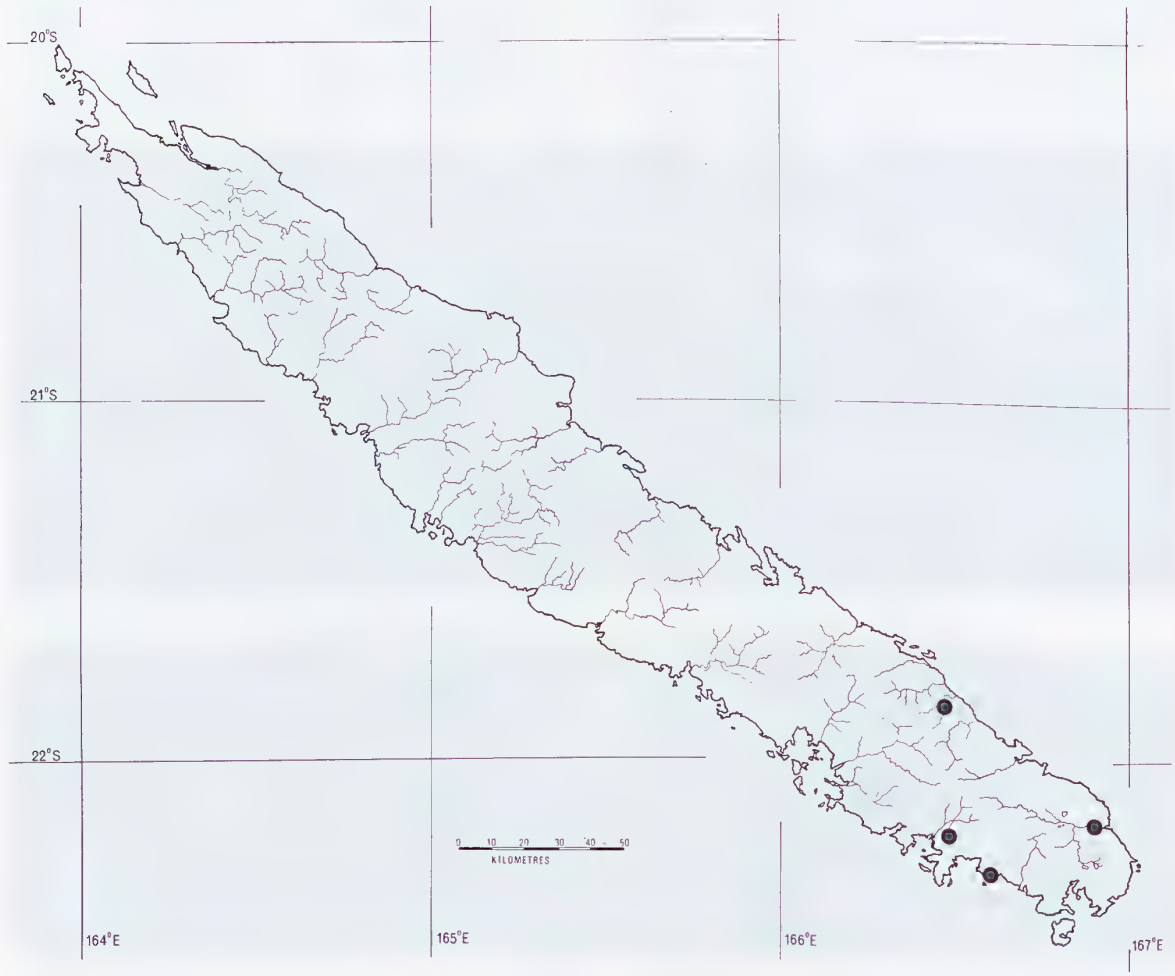


Fig. 71. Distribution of *Sigaloseps deplanchei* in New Caledonia.

as scaled, i.e. traversed by fine longitundinal sutures. The discrepancy between Bavay's type material and description of the lower eyelid of this taxon may be more a matter of interpretation, although *S. deplanchei* from the west coast usually have an undivided semi-transparent disc in the lower eyelid.

Boulenger (1887) and Roux (1913) both redescribed *Lygosoma deplanchei* Bavay, and correctly placed *Hinulia tetragonurus* Günther in its synonomy.

Genus *Cryptoblepharus* Wiegmann

Cryptoblepharus Wiegmann, 1834: 12 (type species *Cryptoblepharus poecilioplеurus* Wiegmann).

Diagnosis. Small skinks, maximum SVL approximately 50 mm; head and body depressed in form; frontoparietals fused; supranasals generally absent; lower eyelid ablepharine; atlantal arches fused to intercentrum.

Recognized species. Greer (1974) listed a single species with 36 subspecies. Most of these taxa are now recognized as distinct species. Storr (1976) has since described the Australian species *C. carnabyi* and *C. megastictus,* and Covacevich & Ingram (1978) *C. fuhni.*

Cryptoblepharus novocaledonicus Mertens

Figs 72–74

Ablepharus peronii Bavay, 1869: 31.
Cryptoblepharus boutonii novo-caledonicus Mertens, 1928: 88.

Type material. HOLOTYPE: SMF 15520. Not examined but topotypic material from the vicinity of Hienghene is included in the specimens examined here.

Material examined. AM R78008-26, Mouac Island off Poum, 20°13′S 164°00′E; NHMB 7213-16, Pam, 20°15′S 164°18′E; AM R77915, 21 km north of Puebo on coast road, 20°17′S 164°26′E; AM R77916-20, beach front 9 km north of Heinghene, 20°38′S 160°53′E; AM R77897-902, beach below gendarmarie at Heinghene, 20°42′S 164°55′E; NHMB 7217-18, 7220-22, Hienghene, 20°41′S 164°56′E; AM R78220-28, beach front 3 km south of La Fausse Yate bridge, 22°10′S 166°57′E; AM R77508-18, 78094-106, Anse de Kuendu, Isle Nou, 22°15′S 166°23′E; AM R78289-303, 2 km west of Plum turnoff on Mt Dore road, 22°17′S 166°37′E; AM R110208, Porc-Epic Island, 22°19′S 166°36′E; AM R110211-19, Petit Mato Island off Noumea, 22°32′S 166°46′E; AM R110220-21, Grand Mato Island off Noumea, 22°33′S 166°48′E.

Description. This description is based on 65 adult specimens.

MEASUREMENTS: maximum SVL 43 mm; distance from axilla to groin 48.5–58.5% of SVL ($\bar{x}$ = 53.8, n = 65); hindlimb length 40–54.7% of SVL ($\bar{x}$ = 45.7, n = 64); tail length ca. 142.1–151.5% of SVL ($\bar{x}$ = 146.8%, n = 2).

SCALATION: frontonasal broader than long (W/L 111.1–150%, $\bar{x}$ = 130.8, n = 63); frontal almost as broad to slighty broader than long (W/L 77.7–121%, $\bar{x}$ = 97, n = 63); prefrontals large, usually in moderate to broad contact (89.2%, n = 65) (fused medially in one individual), rarely in narrow to point contact only; frontoparietal and interparietal fused to form a single

Fig. 72. *Cryptoblepharus novocaledonicus* from Isle Mouac.

scale; parietals each bordered by a single enlarged nuchal and upper temporal scale.

Nasals moderately to widely separated, with moderate to prominent postnasal crease (95.4%, n = 65), rarely a distinct supranasal; 2 loreals in a horizontal sequence, anterior near as deep as broad, posterior broader than deep and shallower than anterior loreal; anterior subocular single; upper labials 7 (92.1%, n = 65), with fifth subocular and contacting lower eyelid, rarely 6 (2.4%) or 8 with fourth and sixth respectively subocular; last upper labial occasionally divided (10.4%) by an oblique transverse suture; primary temporal single; upper and lower secondary temporals single; tertiary temporals fused to form a single, elongate scale; postlabials 2; lower labials usually 6 (90.5%, n = 65), rarely 5 (1.6%), 7 (7.1%) or 8, first 2 contacting postmental; chinshields 3, first pair in moderate to broad contact.

Lower eyelid largely a clear disc nearly completely covering eye, surrounded on lower, anterior and posterior edges by small granular scales, bordered uppermost by several distinct, enlarged upper palpebrals.

Ear opening with numerous small, blunt, lobules around edges, largely obscured by overlapping scales anteriorly.

Body scales smooth; midbody scale rows 22–26 ($\bar{x} = 23.8$, sd = 1, n = 65); paravertebral scales 52–62 ($\bar{x} = 55.7$, sd = 2.1, n = 65).

Lamellae beneath fourth toe 18–25 ($\bar{x} = 21.1$, sd = 1.6, n = 65).

OSTEOLOGY: presacral vertebrae 27; postsacral vertebrae ca. 44 (n = 1); phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4, respectively.

COLOUR AND PATTERN: dorsal surface light to mid brown, always with a concentration of dark brown to black flecks along laterodorsal area (most prominent anteriorly), darker coloured individuals sometimes also with darker flecks extending over remainder of posterior part of dorsum; head light to mid brown similar to dorsal base colour, but with a copperish tinge and darker flecks and edging to sutures. Pale dorsolateral

Fig. 73. Distribution of *Cryptoblepharus novocaledonicus* (closed circle) in New Caledonia.

Fig. 74. Coastal rock outcroppings inhabited by *Cryptoblepharus novocaledonicus* on the **(a)** north coast in vicinity of Poum, and **(b)** south-east coast limestone outcropping near Yate.

stripe cream with an olive tinge, well defined anteriorly to midbody, tending to become obscure posteriorly. Lateral surface dark brown to black (same as laterodorsal markings), uppermost with obvious pale spotting for entire length, tending to become less well defined and generally lighter approaching hindlimbs; mid to lower lateral surfaces light to mid brown (usually same as dorsal surface) with light flecking overall and dark flecks more obvious on lower lateral surface, thus appearing as a poorly defined pale midlateral stripe extending from level of ear to hindlimb in boldly marked individuals. Limbs similar to dorsal surface above, unmarked below; soles of feet cream with brown calli anteriorly; lamellae cream with black blotching and brown calli for most of digit length, tending to lack calli distally. Venter pale, without markings.

Distribution and habitats. *Cryptoblepharus novocaledonicus* is recorded from a number of localities on the east, north-west and south-west coasts of the New Caledonian mainland, and islands off the north and south-west coasts (Fig. 73). Roux (1913) also records the species from Mare Island in the Loyalty Islands group. The apparent absence of *C. novocaledonicus* from most of the west coast is most likely lack of collecting in this region. This species would be expected to occur in suitable coastal habitat on this part of the mainland as well as other offshore islands.

On the coast, *C. novocaledonicus* inhabits rocky beach front habitat (Fig. 74) where it is usually observed active amongst boulders or on rock ledges around headlands.

Reproduction. *Cryptoblepharus novocaledonicus* is oviparous; two eggs are produced, one in each oviduct.

Genus *Nannoscincus* Günther

Anotis Bavay, 1869: 29 (type species *Anotis mariei,* Bavay, 1869).

Nannoscincus Günther, 1872: 421 (type species *Nannoscincus fuscus,* Günther, 1872 = *Nannoscincus mariei).*

Diagnosis. *Nannoscincus* is a member of the *Eugongylus* group of Greer (1979). It can be distinguished from all other genera in that subgroup by the following combination of characters: small size (maximum SVL less than 50 mm) and body form elongate with limbs failing to meet when adpressed; supranasals absent; prefrontals absent, or diminutive and widely separated; upper labials 6, fourth subocular and contacting granules of lower eyelid; single pair of enlarged nuchals; ear opening greatly reduced or absent; phalangeal formula of forelimbs 2.3.4.4.3 for *N. maccoyi, N. greeri, N. rankini* and *N. mariei,* or further reduced to 2.3.3.3.2 in *N. gracilis* and 0.3.3.3.2 in *N. sleveni.*

Recognized species. *Nannoscincus mariei* (Bavay, 1869); *N. gracilis* (Bavay, 1869); *N. maccoyi* (Lucas & Frost, 1894); *N. sleveni* (Loveridge, 1941); *N. rankini* n. sp. and *N. greeri* n. sp.

Remarks. Czechura (1981), in reviewing the status of *Lygosoma graciloides* Lönnberg & Andersson, 1913, confirmed Cogger's (1979) suggestion that the generic name *Anotis* Bavay, 1869, was preoccupied by *Anotis* Rafinesque, 1815, and that the next available generic name for the type species *mariei* is *Nannoscincus* Günther, 1872.

Key to Species of New Caledonian *Nannoscincus*

1. Ear opening small but discernable; first supraciliary contacts frontal; colour dichromatic with light dorsal and dark lateral surfaces well defined. 2

——Ear opening absent, external ear completely scaled over; first supraciliary usually separated from frontal; colour dark with little definition between lateral and dorsal surfaces. ..... *N. mariei*

2. Lower eyelid scaly; frontoparietals distinct. 3

——Lower eyelid with a distinct semi-translucent central area; frontoparietals fused. 4

3. Forelimb pentadactyl. ..... *N. gracilis*

——Forelimb tetradactyl. ..... *N. sleveni*

4. Phalangeal formula for pes 2.3.4.5.4. ..... *N. greeri*

——Phalangeal formula for pes 2.3.4.4.3. ..... *N. rankini*

Nannoscincus mariei (Bavay)
Figs 75–80

Anotis mariei Bavay, 1869: 29.
Nannoscincus fuscus Günther, 1872: 421.

Type material. LECTOTYPE: *Anotis mariei* Bavay, BM 1946.8.17.79, here designated, SVL 33.5 mm (Fig. 75). One of two original syntypes BM 1946.8.17.79-80 both from New Caledonia. HOLOTYPE: *Nannoscincus fuscus* Günther, BM 1946.8.16.16, SVL 35.5 mm, (Fig. 77), recorded as from "Feejee Islands" in type description, later ammended to "New Caledonia" in BM catalogue.

Additional material examined. NHMB 7228, 7230-31, Ngoi Tal (700 m), 21°49′S 166°36′E; QM J43998, Mt Dzumac (700 m), 22°03′S 166°28′E; NHMB 7223, BM 1926.9.17.55, MCZ 112223, Mt Mou, 22°04′S 166°21′E; ZFMK 25455, north-east of Noumea; NHMB 7224-27, Yate, 22°09′S 166°54′E; AM R78142, 4 km up the Mt Gouemba road (300–350 m), near Yate, 22°09′S 166°54′E; CAS 158358-62, QM J44004-05 (400 m), Mt Koghis, 22°19′S 166°32′E; MCZ 46173, Yahoue Valley near Noumea, 22°12′S 166°30′E; MCZ 92393, Noumea, 22°16′S 166°27′E; MCZ 19605, Ngoi Valley; QM J43999, Foret Thy Reserve (150 m).

Diagnosis. *Nannoscincus mariei* can be distinguished from all other members of the genus by the following combination of characters: frontoparietals distinct; loreal single; ear opening absent; lower eyelid scaly; forelimbs pentadactyle; phalangeal formula for manus 2.3.4.4.3; phalangeal formula for pes 2.3.4.4.3; little distinction between dark dorsal and lateral colour.

This species is further distinguished from all other *Nannoscincus* by having a distinctive sheath-like scale on distal tips of digits (Fig. 78).

Description. This description is based on 14 adult specimens (including lectotype of *A. mariei* Bavay and holotype of *N. fuscus* Günther).

MEASUREMENTS: maximum SVL 37.5 mm; distance from axilla to groin 60–67.1% of SVL ($\bar{x} = 63$, n = 12); hindlimb length 17.9–23.2% of SVL ($\bar{x} = 21.5$, n = 12); tail length 88.5–101.5% of SVL ($\bar{x} = 94.3$, n = 7).

SCALATION: frontonasal broader than long (W/L 130.4–183.8%, $\bar{x} = 149.4$, n = 12); prefrontals very small, moderately to widely separated (NHMB 7226 absent both sides); frontal narrow and long; frontoparietals distinct; interparietal distinct; parietals each bordered by a single nuchal and upper secondary temporal scale; primary temporal single; upper and lower secondary temporals single; tertiary temporals 2.

Nasals moderately separated, usually contacting first upper labial only (76.2%, n = 12), occasionally in narrow to point contact with second upper labial; loreal single, deep as nasal; anterior subocular single; supraciliaries usually 7 (83.3%, n = 12), 8 (12.5%) or 6, first usually failing to contact frontal (77.8%); upper labials usually 6 (91.7%, n = 12) with fourth subocular, rarely 7 with fifth subocular; postlabials 2; lower labials

Fig. 75. BM 1946.8.17.79, lectotype of *Anotis mariei* Bavay.

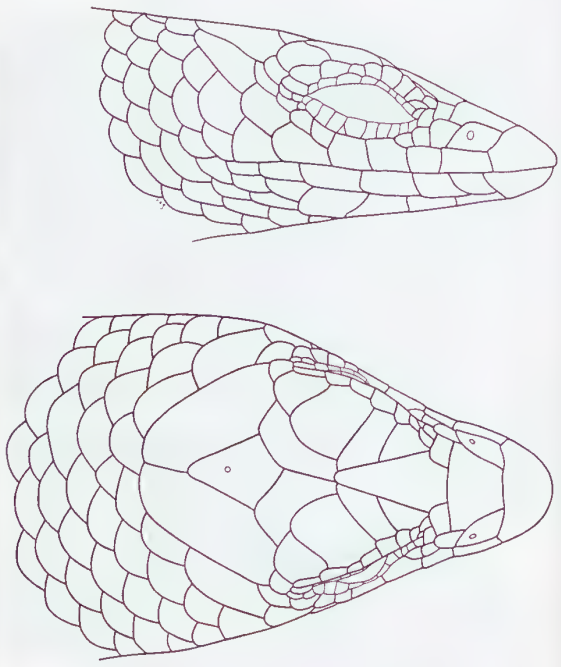


Fig. 76. Lateral and dorsal views of the head of NHMB 7224, a specimen of *Nannoscincus mariei* (Bavay).

Fig. 77. BM 1946.8.16.16, holotype of *Nannoscincus fuscus* Günther.

5, first 2 in contact with postmental; chinshields 3.

Lower eyelid scaled, appearing as a large smooth opaque shield with fine longitudinal sutures running from upper palpebral rim to near base, and with band of fine granulated scales about anterior, posterior and ventral margin.

External ear opening absent.

Dorsal body scales usually with 4 fine striations, laterals more or less smooth; midbody scale rows 18–22 ($\bar{x}$ = 20, sd = 1.5, n = 14); paravertebral scales 49–56 ($\bar{x}$ = 52.2, sd = 1.7, n = 12).

Lamellae beneath fourth toe 10–13 ($\bar{x}$ = 11.1, sd = 0.9, n = 12), often fragmented basally; distal tip of each digit with a distinctive, enlarged sheath-like scale (Fig. 78) within which the claw apparently retracts, i.e., claws barely visible in some individuals (apparently almost fully withdrawn) to short and blunt but moderately obvious in others.

OSTEOLOGY: premaxilliary teeth 11 (n = 2); maxillary teeth 18–19 ($\bar{x}$ = 18.5, sd = 0.5, n = 2); dentary teeth 21–24 ($\bar{x}$ = 23, sd = 1.2, n = 2); presacral vertebrae 29–31 ($\bar{x}$ = 30.4, sd = 0.7, n = 7); postsacral vertebrae 31 (n = 1); phalangeal formula for manus and pes 2.3.4.4.3 and 2.3.4.4.3, respectively.

COLOUR AND PATTERN: in alcohol dark brown all over, slightly lighter on lateral and ventral surfaces. Both Roux (1913) and Bavay (1869) make reference to a series of dorsal lines consisting of numerous dark flecks longitudinally aligned, this condition sometimes extending laterally.

Comments on lower eyelid morphology in *Nannoscincus*. Bavay's syntypes of *Anotis mariei* and *Lygosoma gracilis* agree with his description (1869) and the redescriptions of Boulenger (1887) and Roux (1913) in all but the condition of the lower eyelid, which Bavay and Boulenger describe as transparent over part of its surface, and to which Roux makes no reference. Günther (1872) describes the lower eyelid of *Nannoscincus fuscus* as being scaled, but makes no mention of this feature in the description of *Mocoa micropus*.

The lower eyelid of *N. mariei, N. gracilis* and *N. sleveni* is distinguished as scaly by: lacking a row of

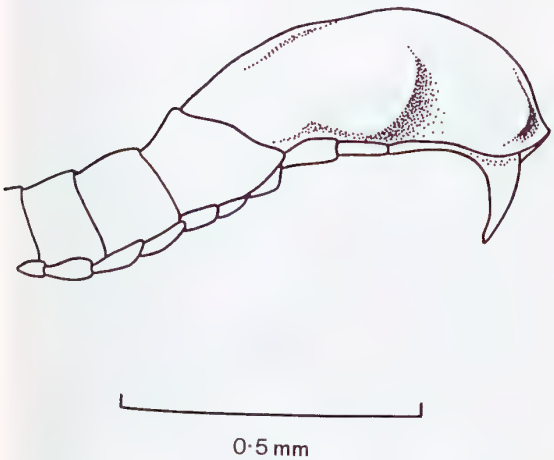


Fig. 78. Distal tip of the fourth digit of hindlimb of *Nannoscincus mariei* (AM R78142) showing enlarged sheathing scale and claw.

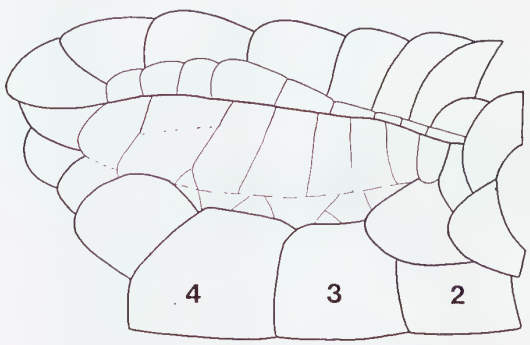


Fig. 79. Details of the scaled lower eyelid typical of *N. mariei, N. sleveni* and *N. gracilis* (AM R77717, *N. gracilis* pictured; upper labials numbered, 2 is anteriormost figured). Note lack of sutures uppermost failing to define palpebral rim.

distinct palpebral scales above, having instead a dark palpebral rim in obvious contrast to flatter opaque sector of eyelid immediately below; having the palpebral rim and sector of lower eyelid below palpebral rim divided by fine sutures, giving a series of adjacent rectangular scales higher than wide and bordered at the lower edge by smaller raised granules (Fig. 79). Sutures may be positioned anteriorly or posteriorly to centre of eyelid, appearing as a large central scale bordered by smaller scales. In extreme cases median sutures may be absent or so far displaced as to resemble an opaque windowed lower eyelid.

Distribution and habitats. *Nannoscincus mariei* is confined to the southern section of mainland New Caledonia (Fig. 80).

Bavay (1869) describes this species as living in montane forests in very shady and humid places, under stones partly buried in mud near streams. Roux (1913) describes it as occurring from the edge of the sea to mountains, living under rocks on the forest floor. The single specimen from our collection (AM R78142) was found on Mt Gouemba (c.a. 560 m) south of Yate on the east coast, under a rock in a rainforest thicket of a small gully (Fig. 18).

Remarks. Both Boulenger (1887) and Roux (1913) redescribed *Lygosoma mariae* (Bavay), and correctly placed *Nannoscincus fuscus* Günther in its synonomy.

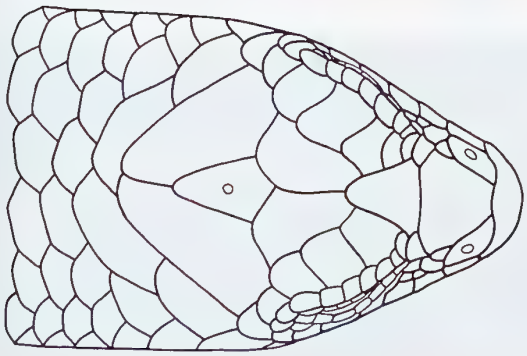
Nannoscincus gracilis (Bavay)
Figs 79–84

Lygosoma gracilis Bavay, 1869: 24.
Mocoa micropus Günther, 1872: 420.

Type material. LECTOTYPES: *Lygosoma gracilis* Bavay, BM 1946.8.17.64, here designated, SVL 33 mm, 4 instead of 5 digits on right hand, second digit reduced to a stump. One of two original syntypes, BM 1946.8.17.63-64, both from New Caledonia. *Mocoa micropus* Günther, lectotype BM 1946.8.16.80 here designated, SVL 33 mm. One of two original syntypes, BM 1946.8.16.80-81, recorded as from "Feejee

Fig. 80. Distribution of the genus *Nannoscincus* in New Caledonia: *N. gracilis* (closed circle); *N. sleveni* (open circle); *N. rankini* (open star); *N. rankini* and *N. gracilis* from same immediate area (open star in closed circle); *N. greeri* (open triangle); *N. greeri* and *N. gracilis* from same immediate area (open triangle in closed circle); *N. mariei* (open square).

Fig. 81. *Nannoscincus gracilis* from Mt Aoupinie forestry camp (500 m), New Caledonia.



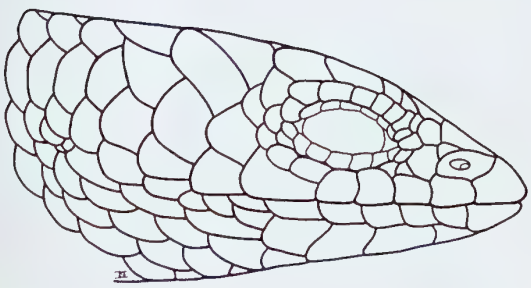


Fig. 82. Lateral and dorsal views of the head of BM 1946.8.17.64, lectotype of *Lygosoma gracile* Bavay.

Islands" in type description, later ammended to "New Caledonia" in BM catalogue.

Additional material examined. CAS 157685-89 (east slope), 158522-23 (northeast slope), Mt Koyaboa, Poindimie, 20°56′S 165°20′E; AM R77733, 3 km north-east of Mt Aoupinie forestry camp by road, 21°07′S 165°22′E; AM R77688, 2 km north-east of Mt Aoupinie forestry camp by road (500 m), 21°08′S 165°21′E; AM R77717-19, AM R77783, 1 km north-east of Mt Aoupinie forestry camp (500 m), 21°08′S 165°21′E; AM R77656-57, AM R77771, Mt Aoupinie forestry camp (500 m), 21°08′S 165°21′E; AM R77745-46, summit of Mt Aoupinie (1086 m), 21°11′S 165°16°E; ZFMK 25439, Houailou, 21°17′S 165°37′E; BM 1926.9.17.57, Houailou Valley; AM R77541-42, 2 km north of Poya road junction on Bourail to Houailou road, 21°24′S 165°26′E; NHMB 7241, Boreare (200 m), 21°22′S 165°28′E; QM J43996-97, Col d' Amieu forest station (400 m), 21°37′S 165°48′E; NHMB 7243-45, La Foa (100 m), 21°43′S 165°49′E; AM R77454, Fambourg Blanchot, Noumea, 20°18′S 166°27′E; QM J44001, Foret Thy Reserve (150 m).

Diagnosis. *Nannoscincus gracilis* can be distinguished from all other members of the genus by possessing the following combination of characters: frontoparietals distinct; anterior and posterior loreal present; ear opening minute; lower eyelid scaly; forelimbs pentadactyl; phalangeal formula for manus 2.3.3.3.2; phalangeal formula for pes 2.3.4.4.3; dorsal colour distinctly lighter than lateral colour.

Description. This description is based on 26 adult specimens (from those listed above, but not including CAS 157685-89, CAS 158522-23 and BM 1926.9.17.57).

MEASUREMENTS: maximum SVL 49 mm; distance from axilla to groin 62–70.4% of SVL ($\bar{x} = 67.2$, $n = 24$); hindlimb length 16.6–23.3% of SVL ($\bar{x} = 19.5$,

n = 25); tail length ca. 73.5–89.5% of SVL ($\bar{x}$ = 80, n = 4).

SCALATION: frontonasal broader than long (W/L 133.3–175.6%, $\bar{x}$ = 150.7, n = 14); prefrontals very small, widely separated; frontal slightly longer than wide (W/L 65.8–93.7%, $\bar{x}$ = 75.8, n = 13); frontoparietals distinct; interparietal distinct; parietals each bordered by a single nuchal and upper secondary temporal; primary temporal single; upper and lower secondary temporals single; tertiary temporals 2.

Nasals moderately separated, broadly contacting first upper labial; anterior loreal usually present as a semilunar scale on posterodorsal margin of nasal failing to contact upper labials (91.7%, n = 24), occasionally extending its lower edge to contact upper labials; posterior loreal wide dorsally and narrow basally, usually contacting upper labials basally (60.4%, n = 24) and anterior loreal and nasal (when anterior loreal fails to contact labials) anteriorly; lower preocular large and elongate, occupying area below and adjacent to posterior loreal and extending anteriorly to contact either first upper labial only, or first upper labial and nasal (33.3%, n = 24 when both posterior and anterior loreals are excluded from contact with upper labials); anterior subocular usually single (92.7%, n = 21), occasionally followed by smaller scale; supraciliaries 7 (94.2%, n = 26), with first narrow and contacting frontal, rarely 6; upper labials usually 6 (88.5%, n = 26) with fourth subocular, occasionally 7 with fifth subocular; postlabials 2; lower labials 6, first 2 in contact with postmental; chinshields 3, first pair in broad contact.

Lower eyelid scaled, a large smooth opaque shield with fine longitudinal sutures running from palpebral rim to near base, and with a band of fine granulated scales about anterior, posterior and ventral margin (in a large number of specimens examined the lower eyelid is fixed down in position leaving only palpebral rim and uppermost section of eyelid in view, therefore the condition of lower eyelid could not be determined). The syntypes of both *Lygosoma gracilis* and *Mocoa micropus* have the median sutures lost to produce an off-centre and larger than normal opaque shield.

Ear opening extremely small, lacking auricular lobules, and partially hidden by over lapping anterior scale.

Dorsal scales usually with 3 fine striations or smooth, lateral scales usually with 2 weak striations or smooth; midbody scale rows 20–26 ($\bar{x}$ = 22.7, sd = 1.6, n = 26); paravertebral scales 53–65 ($\bar{x}$ = 59.7, sd = 2.9, n = 26).

Lamellae beneath fourth toe 9–14 ($\bar{x}$ = 11.3, sd = 1.2, n = 26).

OSTEOLOGY: premaxillary teeth 11 (n = 5); maxillary teeth 25–26 ($\bar{x}$ = 25.2, sd = 0.4, n = 5); dentary teeth 32–34 ($\bar{x}$ = 33.6, sd = 0.8, n = 5); presacral vertebrae 33–34 ($\bar{x}$ = 33.5, sd = 0.5, n = 17); postsacral vertebrae

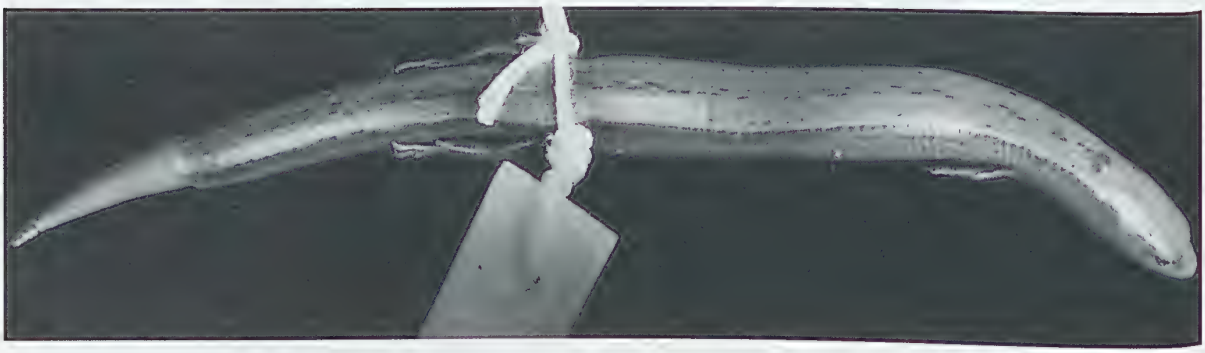


Fig. 83. BM 1946.8.17.64, lectotype of *Lygosoma gracile* Bavay.

Fig. 84. BM 1946.8.16.80, lectotype of *Mocoa micropus* Günther.

36 (n = 1); phalangeal formula for manus and pes 2.3.3.3.2 and 2.3.4.4.3, respectively.

COLOUR AND PATTERN: dorsal surface light brown with several dark, longitudinally aligned blotches on nape, reduced posteriorly to a series of fine flecks forming a faint vertebral stripe extending posteriorly to basal part of tail. Dorsolateral stripe fine, dark and defining dorsal and lateral surfaces, extending posteriorly from eye to be deeply inflected over tympanic region, continuing past level of hindlimbs and along tail as a series of dark elongate blotches. Lateral surface grading from mid to light brown from upper to lower, tending towards grey near venter. Side of head dark brown, rostral with black midrostral streak. Venter pale with light brown centre to each scale; lower labials and chinshields brown-edged.

Variation in dorsal and lateral colour occurs with some individuals being lighter or darker than described.

Distribution and habitats. *Nannoscincus gracilis* occurs mainly in rainforest regions of the central coast and mountains of mainland New Caledonia.

Bavay (1869) records this species from sandy forest near the coast. Roux's (1913) records were from localities also near the coast and to 700 m. AM specimens were collected from under and in rotting logs in rainforest, and occasionally under small stones. It was also recorded from dry scrub of suburban Noumea on the west coast (Fig. 80).

Reproduction. All AM female specimens collected December 1978, were gravid, having 1–3 yolked ovarian follicles or fully shelled oviducal eggs. Presence of shelled eggs indicate this species is proabably oviparous.

Remarks. Both Boulenger (1887) and Roux (1913) redescribed *Lygosoma gracile* Bavay, correctly placing *Mocoa micropus* Günther in its synonomy.

Nannoscincus sleveni (Loveridge)
Figs 79–81, 85, 86

Lygosoma sleveni Loveridge, 1941: 193.

Type material. HOLOTYPE: *Lygosoma sleveni* Loveridge, MCZ 9295, SVL 41 mm; TL 29 mm regenerated, colour and pattern with overall greenish tinge (artifact of preservative).

Additional material examined. NHMB 7239-40, Negropo Tal (100 m), 21°32′S 165°54′E; NHMB 7232-33, NHMB 7236-38, AM R6665, Mt Kanala (700 m), 21°35′S 165°56′E.

Diagnosis. *Nannoscincus sleveni* can be distinguished from all other members of the genus by the following combination of characters: frontoparietals distinct; anterior and posterior loreals present; ear opening minute; lower eyelid scaly; forelimbs tetradactyl,

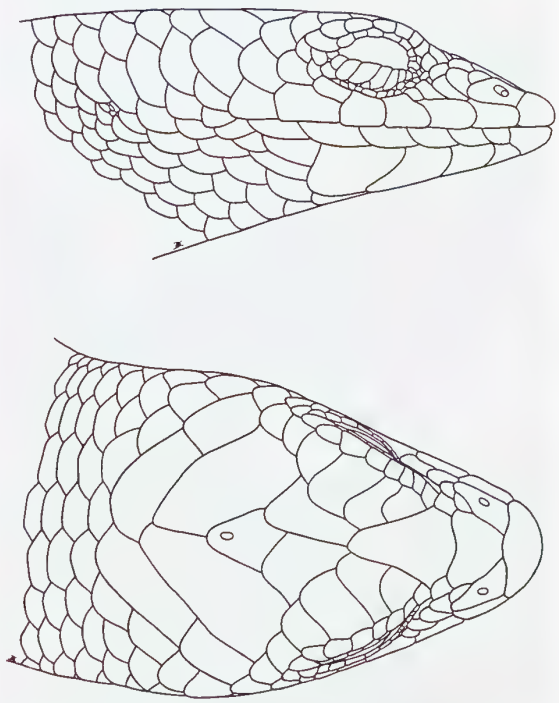


Fig. 85. Lateral and dorsal views of the head of MCZ 9295, holotype of *Lygosoma sleveni* Loveridge.

Fig. 86. MCZ 9295, holotype of *Lygosoma sleveni* Loveridge.

phalangeal formula for manus 0.3.3.3.2; phalangeal formula for pes 2.3.4.4.3; dorsal colour distinctly lighter than lateral colour.

Description. MEASUREMENTS: maximum SVL 43 mm; distance from axilla to groin 62–65% of SVL ($\bar{x}$ = 63.4, n = 6); hindlimb length 20.5–22.2% of SVL ($\bar{x}$ = 21.7, n = 6); tail length ca. 82.5–96.4% of SVL ($\bar{x}$ = 88, n = 3).

SCALATION: head shield configuration similar to *N. gracilis;* frontonasal broader than long (W/L 118.2–156%, $\bar{x}$ = 140.2, n = 5), prefrontals very small, widely separated; frontal slightly longer than wide; frontoparietals distinct; interparietal distinct; parietals each bordered by a single nuchal and upper secondary temporal; primary temporal single; upper and lower secondary temporals single; tertiary temporals 2.

Nasals moderately separated, contacting first upper labial only; anterior loreal a semilunar scale positioned on posterodorsal margin of nasal, failing to contact upper labials; posterior loreal wide dorsally and narrow basally, usually contacting first upper labials basally and anterior loreal and nasal anteriorly; lower preocular large and elongate, occasionally extending forward to contact first upper labial and nasal (14.3%, n = 6), thereby excluding both anterior and posterior loreals from contact with upper labials; upper labials usually 6 (83.3%, n = 6) with fourth subocular, occasionally 7 with fifth subocular; postlabials 2; lower labials 6, first 2 usually in contact with postmental, holotype with postmental contacting first lower labial only.

Dorsal scales with 3 fine striations; midbody scale rows 22–26 ($\bar{x}$ = 24, sd = 1.6, n = 6); paravertebral scales 57–64 ($\bar{x}$ = 60.3, sd = 2.6, n = 6).

Lamellae beneath fourth toe 11–13 ($\bar{x}$ = 12.2, sd = 0.6, n = 6).

OSTEOLOGY: presacral vertebrae 31–34 ($\bar{x}$ = 32.2, sd = 0.9, n = 6); phalangeal formula for manus and pes 0.3.3.3.2 and 2.3.4.4.3, respectively.

Distribution. *Nannoscincus sleveni* is known only from two localities on the south-east coast of mainland New Caledonia: Negropo Tal (100 m) and Mt Kanala (700 m) (Fig. 80).

Remarks. Loveridge (1941) described *Lygosoma sleveni* from specimens collected by Roux & Sarasin in 1911 and previously identified by Roux in 1913 as *Lygosoma gracile*. He differentiated it from *Nannoscincus gracilis* on the basis of four digits on the forelimbs instead of five, and 22–26 vs 20 midbody scale rows. Only the first of these diagnostic characters is consistent; *N. gracilis* examined in this study possess 20–24 midbody scale rows.

Nannoscincus rankini n. sp.

Figs 80, 87–89

Type material. HOLOTYPE: AM R77736, adult male from summit of Mt Aoupinie (1086 m), New Caledonia, 21°11′S 165°16′E, collected by R. Sadlier & P. Rankin, 14 Dec 1978. PARATYPE: AM R77814, Kavatch forestry camp, New Caledonia, 20°42′S 164°50′E, collected by R. Sadlier & P. Rankin, 16 Dec 1978.

Diagnosis. *Nannoscincus rankini* can be distinguished from all other members of the genus by the following combination of characters: frontoparietals fused; loreal single; ear opening minute; lower eyelid with semi-translucent window; forelimbs pentadactyl; phalangeal formula for manus 2.3.4.4.3; phalangeal formula for pes 2.3.4.4.3; dorsal colour distinctly lighter than lateral colour.

Etymology. Named for my friend Peter Rankin who died due to an accident while we were collecting reptiles in New Caledonia.

Description. MEASUREMENTS: maximum SVL 37.5 mm; distance from axilla to groin 62.7–63.5% of SVL ($\bar{x}$ = 63.1, n = 2); forelimb to snout length 32–32.4% of SVL ($\bar{x}$ = 32.2, n = 2); hindlimb length 20–24% of SVL ($\bar{x}$ = 22, n = 2); tail length ca. 83.8% of SVL (n = 1).

SCALATION: frontonasal broader than long (W/L 164.7–176.5%, $\bar{x}$ = 170.6, n = 2); prefrontals very small

Fig. 87. *Nannoscincus rankini* n. sp. (holotype) from near the summit of Mt Aoupinie, New Caledonia.

and widely separated (holotype) or absent (left absent in AM R77814); frontal short, almost as long as wide; frontoparietals fused; interparietal distinct; parietals each bordered by a single nuchal and upper secondary temporal; primary temporal single; upper and lower secondary temporals single; tertiary temporals 2.

Nasals moderately separated, contacting first upper labial only; loreal single, broader above than at base, in moderate to narrow contact with first and second upper labial; anterior subocular single; supraciliaries 7, first contacting frontal; upper labials 6 with fourth subocular and contacting lower eyelid; postlabials 2; lower labials 5, first 2 contacting postmental; chinshields 3, first pair in broad contact.

Lower eyelid with an obvious, centrally located semi-translucent window, 37.5–39.3% ($\bar{x}$ = 38.4, n = 2) of eye length, palpebral scale row distinct.

Ear opening extremely small, circular and lacking auricular lobules.

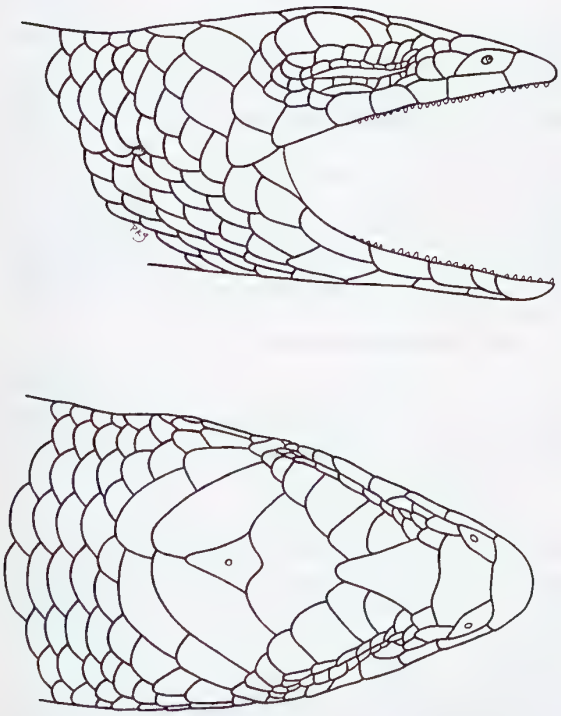


Fig. 88. Lateral and dorsal views of the head of AM R77736, holotype of *Nannoscincus rankini* n. sp.

Dorsal scales smooth (AM R77814) or with 3–4 fine striations (holotype), laterals smooth or with progressively weaker striations; midbody scale rows 22–24 ($\bar{x}$ = 23, sd = 1, n = 2); paravertebral scales 49–52 ($\bar{x}$ = 50.5, sd = 1.5, n = 2).

Lamellae beneath fourth toe 12–14 (n = 2).

OSTEOLOGY: premaxilliary teeth 11 (n = 2); maxillary teeth 23–25 ($\bar{x}$ = 23.7, sd = 0.9, n = 2); dentary teeth 28–29 ($\bar{x}$ = 28.7, sd = 0.5, n = 2); presacral vertebrae 29–30 ($\bar{x}$ = 29.5, sd = 0.5, n = 2); phalangeal formula for manus and pes 2.3.4.4.3 and 2.3.4.4.3 (n = 2), respectively.

COLOUR AND PATTERN: dorsal surface either mid brown with faint but continuous darker vertebral stripe extending from nape posteriorly to just past hindlimbs, thence fading into darker dorsal colour of tail (holotype), or light brown-grey above with a single, dark blotch on nape (AM R77814). Dorsolateral stripe fine, dark and defining the dorsal and lateral surfaces, extending from posterior canthus of eye to be deeply inflected over tympanic region, then broadening and continuing posteriorly past level of hindlimbs and along tail. Lateral surface dark brown, paling to light brown ventrolaterally. Side of head dark brown, passing onto supraocular area on top of head; rostral brown with a faint, dark midrostral streak. Venter pale and immaculate (holotype), or with faint brown spotting (AM R77814); lower labials brown, chinshields with fine brown spotting.

Distribution and habitats. *Nannoscincus rankini* is known from only two locations on mainland New Caledonia, one on the central highlands, the other on the north-east coast (Fig. 80).

Known habitat preferences differ markedly. The holotype was collected beneath a rock on the roadside at summit of Mt Aoupinie (1086 metres asl) in low heath, whereas AM R77814 was taken from beneath a small rock alongside a creek flowing through hillside rainforest adjacent to the Heinghene River near sea level. *Nannoscincus rankini* is syntopic with *N. gracilis* at Mt Aoupinie.

Nannoscincus greeri n. sp.

Figs 80, 90–91

Type Material. HOLOTYPE: CAS 159606, adult from lower east slope of Mt Koyaboa, Poindimie, ca. 20°56′S 165°20′E, collected by A. Bauer, 1 Jan 1986. PARATYPES: CAS 159607, same collection data as holotype; CAS 158524-26, north-east slope of Mt Koyaboa, Poindimie, 20°56′S 165°20′E, collected

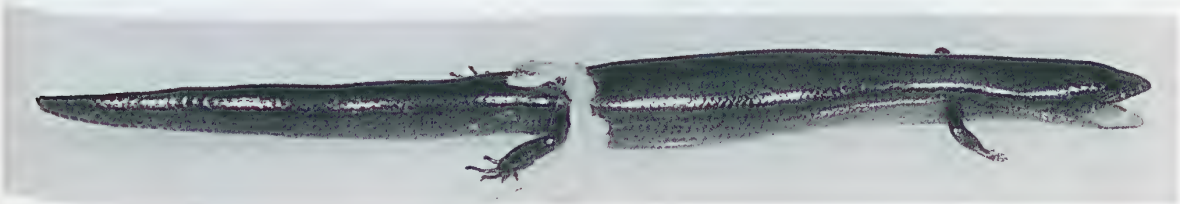


Fig. 89. AM R77736, holotype of *Nannoscincus rankini* n. sp.

A. Bauer & L. Wishmey 1-2 June 1985; MCZ 112224, Houailou valley, collected P.D. Montague.

Diagnosis. *Nannoscincus greeri* can be distinguished from all other members of the genus by the following combination of characters: frontoparietals fused; loreal single; ear opening minute; lower eyelid with a semi-translucent window; forelimbs pentadactyl; phalangeal formula for manus 2.3.4.4.3; phalangeal formula for pes 2.3.4.5.4; dorsal colour distinctly lighter than lateral colour.

Etymology. Named for Dr Allen Greer (AM) for his contributions to scincid lizard systematics, particularly the Australian and Pacific fauna, and continous encouragement and assistance throughout the duration of the research and preparation for this revision of the New Caledonian skinks.

Description. *Nannoscincus greeri* is very similar to *Nannoscincus rankini* in superficial morphology, and differs from the latter mainly in having a primitive phalangeal formula for the pes (2.3.4.5.4 vs 2.3.4.4.3).

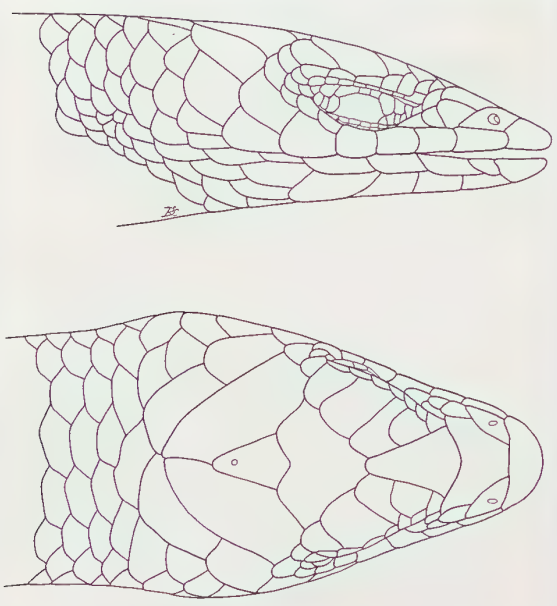


Fig. 90. Lateral and dorsal views of the head of CAS 159606, holotype of *Nannoscincus greeri* n. sp.

MEASUREMENTS: maximum SVL 33.5 mm; distance from axilla to groin 59.7–63.8% of SVL ($\bar{x}$ = 61.2, n = 6); forelimb to snout length 34.8–42.6% of SVL ($\bar{x}$ = 37.5, n = 6); hindlimb length 24.2–26.6% of SVL ($\bar{x}$ = 25.3, n = 6).

SCALATION: frontonasal broader than long (W/L 133.3–165.8%, $\bar{x}$ = 155, n = 5); prefrontals usually absent (75%, n = 6), anterior suture fused to frontonasal, when present very small and widely separated; frontal short almost as long as wide; frontoparietals fused; interparietal distinct; parietals each bordered by a single nuchal and upper secondary temporal; primary temporal single; upper and lower secondary temporals single; tertiary temporals 2.

Nasals moderately separated contacting first upper labial only; loreal single, broader above than at base, in moderate to narrow contact with first and second upper labial; anterior subocular single; supraciliaries 7, first contacting frontal; upper labials 6, with fourth subocular and contacting lower eyelid; postlabials 2; lower labials 5, first 2 contacting postmental; chinshields 3, first pair in broad contact.

Lower eyelid with an obvious centrally located semi-translucent window 39.5–48.7% ($\bar{x}$ = 44.2, n = 5) of eye length, palpebral scale row distinct.

Ear opening extremely small, lacking auricular lobules.

Dorsal scales usually with 3 fine striations, lateral scales usually with 2 weak striations; midbody scale rows 24 (n = 6); paravertebral scales 48–52 ($\bar{x}$ = 50, sd = 1.6, n = 4).

Lamellae beneath fourth toe 15–18 ($\bar{x}$ = 16.6, sd = 1, n = 4).

OSTEOLOGY: no specimens were preserved with the mouth open, dentition was unable to be assessed; presacral vertebrae 29 (n = 6); phalangeal formula for manus and pes 2.3.4.4.3 and 2.3.4.5.4 (n = 6), respectively.

COLOUR AND PATTERN: dorsal surface light to mid brown with some dark flecking anteriorly, particularly on the nape where it encloses a paler (same as dorsal surface) blotch, and on remainder of body as a dark fleck to the median 2 vertebral scale rows, thereby

Fig. 91. CAS 159606, holotype of *Nannoscincus greeri* n. sp.

enclosing a light (same as remainder of dorsal surface), narrow mid vertebral line. Dorsolateral line dark brown, most complete anteriorly and inflected over tympanic region, remainder irregular and broken over most its length, appearing as a single series of bold, dark flecks. Lateral surface light to mid brown (same as dorsal surface) but with each scale having a moderately broad dark fleck forming series of fine, dark longitudinally aligned lines. Side of head dark brown-black, passing onto supraocular region on top of head; temporal and labial regions with pale flecks or spots; rostral with a poorly defined dark midrostral streak or blotch. Venter pale with light to mid brown spotting confined to outer edges and tail.

Distribution. *Nannoscincus greeri* is known from only two locations on the central and northern east coast of mainland New Caledonia (Fig. 80). The habitat preference for this species is unknown.

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References

Andersson, G., 1908. Two new lizards *(Eurydactylus* and *Lygosoma)* from New Caledonia. Arkiv for Zoologi, Band 4. No. 14: 1-5.

Bocage, Barboza du, 1873a. Note sur quelques Geckotiens nouveaux ou peu connus de la Nouvelle Caledonie. Jornal de Sciencias Mathematicas Physicas e Naturaes. Academia Real das Sciencias de Lisboa IV: 201-207.

_____ 1873b. Sur quelques Sauriens nouveaux de la Nouvelle Caledonie et de l'Australie. Journal de Sciencias Mathematicas Physicas e Naturaes. Academia Real das Sciencias de Lisboa IV: 228-232.

_____ 1881. Nota sobre a synonymia de algunas Saurios da Nova Caledonia. Jornal de Sciencias Mathematicas Physicas e Naturaes. Academia Real das Sciencias de Lisboa VIII: 126-132.

Bavay, A., 1869. Catalogue des Reptiles de las Nouvelle - Caledonie et descritpion d'especes nouvelles. Sociéte Linniene de Normandie. Memoires V15.

Böhme, W., 1976. Uber die Gattung *Eugongylus* Fitzinger, mit Beschriebung einer neuen Art (Reptilia: Scincidae). Bonner Zoologische Beitraege 27: 245-251.

_____ 1979. Eine neue Art der Gattung *Leiolopisma* Dumeril and Bibron, 1839 aus neukaledonien (Reptilia: Sauria: Scincidae). Salamandra 15: 140-145.

Borner, R., 1980. Uber neukaledonische Skinke des *Leiolopisma austrocaledonicum*-Komplexes. Miscellaneous Articles in Saurology 5: 1-15.

Boulenger, G.A., 1887. Catalogue of the lizards in the British Museum. (2nd Edition).

Brocchi, M., 1876. Sur un Scincoiden noureau appartenant au genre *Eumeces.* Bulletin Societe Philomathique de Paris (6) 12: 95-97.

Cogger, H.G., 1979. Reptiles and Amphibians of Australia (2nd Edition). Reed, Sydney, 608 pp.

_____ 1986. Reptiles and Amphibians of Australia (4th Edition). Reed, Sydney, 688 pp.

Cogger, H.G., E.E. Cameron & H.M. Cogger, 1983. Zoological Catologue of Australia. Volume 1. Amphibia and Reptilia. Australian Government Publishing Service, Canberra, 313 pp.

Czechura, G.V., 1981. The rare scincid lizard, *Nannoscincus graciloides:* a reappraisal. Journal of Herpetology 15(3): 315-320.

Gill, B., 1986. Collins Handguide to the Frogs and Reptiles of New Zealand. Collins, Auckland, 112 pp.

Greer, A.E., 1974. The generic relationships of the scincid genus *Leiolopisma* and its relatives. Australian Journal of Zoology - Supplementary series 31: 1-67.

_____ 1979. A phylogenetic subdivision of Australian skinks. Records of the Australian Museum 32(8): 339-371.

Günther, A., 1872. LX. On some new species of Reptiles and Fishes collected by J. Brenchley Esq. Annals and Magazine of Natural History 10 (4th series): 421.

Kramer, E., 1979. Typenkatalog der Echsen im Naturhistorischen Museum Basel (BM), Stand 1978. Revue Suisse de Zoologie 86(1): 159-166.

Kluge, A.G., 1967. Systematics, phylogeny and zoogeography of the lizard genus *Diplodactylus* Gray (Gekkonidae). Australian Journal of Zoology 15: 1007–1108.

Loveridge, A.A., 1941. An undescribed skink *(Lygosoma)* from New Caledonia. Proceedings Biological Society of Washington 54: 193–194.

Mertens, R., 1928. Neue Inselrassen von *Cryptoblepharus boutonii* (Desjardin). Sonderabdruck aus dem Zoolog. Anzeiger 78(3/4): 82–89.

_____ 1964. Neukaledonische Riesengeckos (*Rhacodactylus*). Der Zoologische Garten 29: 49–57.

Meier, H., 1979a. Herpetologische Beobachtungen auf Neukaledonien. Salamandra 15: 113–139.

_____ 1979b. Ein lebendgebärender Gecko, *Rhacodactylus trachyrhynchus* Bocage 1873 aus Neukaledonien (Reptilia: Sauria: Gekkonidae). Salamandra 15: 58–60.

Parker, H.W., 1926. A new lizard from New Caledonia. Annals and Magazine of Natural History 18(9): 493–495.

Peters, W., 1870. Uber neue Gattungen und neue oder weniger bekannte Arten von Amphibien. Monatsbericte der Koniglich Preussischen Academie der Wissenchaften zu Berlin: 432–445.

_____ 1879. *Sauroscincus*, eine neue Gattung of Scincoiden aus Neu-Caledonien. Gesellschaft Naturforschender Freunde zu Berlin. Sitzungsberichte 10: 149–150.

Rafinesque, C.S., 1815. Analyse de las Nature ou tableau de l'univers et des corps organises. Palemo.

Roux, J., 1913. Les reptiles de la Nouvelle-Caledonie et des Iles Loyalty. In Nova Caledonia, recherches scientifiques en Nouvelle Caledonie et aux Isles Loyalty, A. Zoologie: 78–160. Wiesbaden (C.W. Kreidel's Verlag).

Sadlier, R.A., 1984. A New Australian Scincid Lizard, *Menetia concinna,* from the Alligator Rivers Region, Northern Territory. Records of the Australian Museum 36: 45–49.

Taylor, E.H., 1935. A Taxonomic Study of the Cosmopolitan Scincoid Lizards of the Genus *Eumeces* with an Account of the Distribution and Relationships of its Species. Bulletin of the University of Kansas 36(14), 642 pp.

United States Board on Geographic Names 1974 New Caledonia and Dependencies and Wallis and Futuna. Official Standard Names. Defence Mapping Agency Topographic Centre, Washington D.C.

Wells, R.W. & C.R. Wellington, 1983. A synopsis of the class Reptilia in Australia. Australian Journal of Herpetology, 1(3–4): 73–129.

Werner, F., 1909. Neue oder seltnere Reptilien des Musée Royal d'Histoire naturelle de Belgique in Brüssel. Zoologische Jahrbücher (Jena) Abteilung für Systematik, Geographie und Biologie der Tiere 28: 263–288.

Zug, G.R., 1985. A new skink (Reptilia: Sauria: *Leiolopisma)* from Fiji. Proceedings of the Biological Society of Washington 98(1): 221–231.

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Aioliops, a New Genus of Ptereleotrine Fish (Pisces: Gobioidei) from the Tropical Indo-Pacific with Descriptions of Four New Species

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ABSTRACT. *Aioliops* is a new genus of ptereleotrine fish that is found on coral reefs from Australia to Indonesia and as far north as the Philippines. Four species compose the genus and all are described as new: *A. brachypterus, A. megastigma, A. novaeguineae* and *A. tetrophthalmus.* These species are readily identifiable by a dark stripe along the dorsolateral surface of the body and a large dark spot on the caudal fin. Osteology of the new genus along with morphology and colour variations of the species are described, and the relationship of *Aioliops* to allied genera is discussed.

RENNIS, D.S. & D.F. HOESE, 1987. *Aioliops,* a new genus of ptereleotrine fish (Pisces: Gobioidei) from the tropical Indo-Pacific with descriptions of four new species. Records of the Australian Museum 39(2): 67–84.

The ptereleotrine gobioids are a group of small, Indo-Pacific fishes that are associated with a variety of habitats, including coral reefs, sand channels and mangrove zones, and are found at depths up to 98 m. These fishes may be seen in large groups, in pairs, or singly, and a few have become popular aquarium species because of their striking colours.

Species of *Aioliops* represent some of the smaller fishes in the subfamily, with the largest mature adults attaining lengths of 24 mm. Unlike *Parioglossus,* which lives primarily in mangrove zones or shallow reef flats and which the new genus superficially resembles, *Aioliops* is found near drop-offs on coral reefs at depths up to 25 m. Fishes of both genera, however, are more likely to be seen in groups rather than singly or in pairs.

Aioliops brachypterus has been collected from the Philippines; *A. megastigma* from Indonesia and the Philippines; *A. novaeguineae* from Papua New Guinea, Irian Jaya and questionably from the Timor Sea; and *A. tetrophthalmus* from tropical eastern Australia. The genus appears to have a limited distribution compared to other related genera, and yet it is not uncommon. Its distribution probably reflects difficulties in capturing individuals as most attempts are thwarted when the fish dart off in different directions. With the use of rotenone, however, groups of 10–30 fish may be collected, although it is just as likely to capture only one or two as the schools often move away when approached. The genus was first collected in 1970, and most of the material has been collected by only five workers.

Classification of the suborder, Gobioidei, based on osteological characters, can be traced back to Regan (1911). Since then, Gosline (1955) placed the microdesmids among the gobioids; Miller (1973) summarized the numerous studies on gobioid classification and proposed another classification; Birdsong (1975) criticized Miller's classification but refrained from proposing an alternate one; Springer (1983) elaborated on the skeletal characters noted by Birdsong and discussed the monophyly of the suborder; and Hoese (1984) recognized 6 families of the suborder and listed characteristic features of each. We follow Hoese (1984) in provisionally placing *Aioliops* in the family Microdesmidae, based on the long posterior pelvic process and single pterygiophore preceding the first hemal spine.

The new genus, *Aioliops,* has been created on the basis of osteological as well as other morphological characters which are not all shared with other ptereleotrines. These characters include: caudal vertebrae having open neural arches with slightly elevated posterior portions and no lateral foramen (except *A. brachypterus* which has closed neural arches

with reduced basal portions and large lateral foramen); a prominent dorsolateral process near the posterior end of the anguloarticular; one pair of interorbital pores; large, ctenoid scales or no scales; and short-based dorsal and anal fins.

The species of *Aioliops* all share the same basic colour pattern which is a dorsolateral stripe along the body and a large, dark caudal-fin spot. Differences in pigmentation exist, and these are often the easiest characteristics to use for distinguishing species.

Aioliops megastigma, A. novaeguineae and *A. tetrophthalmus* are similar in having ctenoid scales, a naked predorsal, three preopercular pores, six spines in the first dorsal fin and four segmented pelvic rays. Of these species, *A. novaeguineae* differs osteologically in having the urostyle fused with the lower hypural plate.

The fourth species, *A. brachypterus,* differs from the others in having no scales, two preopercular pores, five spines in the first dorsal fin and three segmented pelvic rays. It also differs osteologically from the others in having no ventral postcleithrum and closed neural arches on the caudal vertebrae.

Materials and Methods

Measurements and counts follow those described by Hubbs & Lagler (1974) except as noted below. All fish lengths refer to standard lengths (SL). All measurements including standard lengths were taken with an ocular micrometer and recorded to the nearest 0.1 mm. Raw data were converted to percentage of standard length, and t-values of the Students T Test or f-values from Analysis of Variance were computed to determine any significant differences between meristics. Rays refer to segmented rays. The last dorsal and anal ray as counted is branched through the base. The transverse scale count is taken from the anal-fin origin upward and backward to the second dorsal fin. Body depth is taken at the anal-fin origin. Caudal-fin spot length is the distance from the anterior edge to the posterior edge of the spot. Stripe depth is the depth of the lateral stripe at its deepest point below the first dorsal fin. Head-pore counts are from one side of the head (Fig. 1). Comparisons of certain characteristics of the different genera in the subfamily are given in Tables 1 and 2. The following meristic tables are provided for each species: dorsal and anal fins (Table 3); pectoral, pelvic, segmented caudal and branched caudal fins (Table 4); longitudinal and transverse scales (Table 5); circumpeduncle scales and total gill-rakers on the outside face of the first gill arch (Table 6); measurements of the holotypes (Table 7); and morphometric proportions of the four species (Table 8). Vertebrae were counted from radiographs. Osteology was examined from specimens cleared with trypsin and stained with alizarin, and several of these specimens were counter-stained with alcian blue. Illustrations were made with the aid of a camera lucida.

Abbreviations for institutions from which material was examined follow Leviton *et al.* (1985).

Comparative material examined. Material of *Parioglossus* examined is given in Rennis and Hoese (1984). Material other than cleared and stained material of *Ptereleotris* is listed in Randall & Hoese (1985).

Table 1. Comparison of selected characters within the subfamily Ptereleotrinae. (Number after character refers to Fig. 17.)

Character	Genera				
	Aioliops	*Nemateleotris*	*Oxymetopon*	*Parioglossus*	*Ptereleotris*
Segmented dorsal rays	9-12	8-32	26-31	13-19	23-39
Segmented anal rays	9-11	26-31	27-30	13-19	22-37
Pectoral rays	14-18	19-21	20-26	15-20	21-26
Segmented pelvic rays (3)	3-4	5	4	4	4
Longitudinal scales (8)	0 or 37-44 cten/cycl	110-160 cten/cycl	85-105 cten/cycl	0 or 61-109 cycl	121-170 mosly cycl
Filamentous dorsal spines (1)	no	yes	yes or no	yes or no	yes or no
Preopercular pores (9)	2-3	3	3	0, 2	2
Interorbital pore(s)	paired	median	paired	paired	median
Terminal lateral canal pore (10)	+	+	+	-	+
Pterygiophore formula (12)	3(22110)	3(22110)	3(22110)	3(22110)	3(32010)
Jaws	weakly protrusible	weakly protrusible	highly protrusible	highly protrusible	highly protrusible
Body (7)	moderately compressed	moderately compressed	strongly compressed	moderately compressed	moderately compressed

Cleared and stained material. *Nemateleotris decora:* AMS I.19476-045, 50 mm, Yonge Reef, Queensland, Australia. *Nemateleotris magnificus:* AMS I.17027-001, 32 mm, Palau. *Oxymetopon* sp.: AMS (unregistered), 86 mm, Port Moresby, Papua New Guinea. *Ptereleotris evides:* AMS I. 15643-014, 2(51-53 mm), One Tree Island, Queensland, Australia; AMS (unregistered FTL 743), 26 mm, Lizard Island lagoon, Queensland, Australia. *Ptereleotris heteroptera:* AMS I.15682-031, 84 mm, One Tree Island, Queensland, Australia. *Ptereleotris monoptera:* AMS I.15678-007, 70 mm, One Tree Island, Queensland, Australia. *Ptereleotris zebra:* AMS I.15621-012, 4(51-74 mm), One Tree Island, Queensland, Australia.

Other material. *Oxymetopon compressus:* BMNH 1965.11.6.2, 66 mm, HOLOTYPE, Hong Kong. *Oxymetopon typus:* RMNH 4471, 111 mm, HOLOTYPE, Timor. *Oxymetopon* sp.: SIO 80-213, 103 mm, Taiwan; AMS (unregistered), 90 mm, Port Moresby, Papua New Guinea.

Table 2. Comparison of various osteological features of five ptereleotrine genera. (Number after character refers to Fig. 17.)

Character	*Nemateleotris*	*Aioliops*	*Oxymetopon*	*Ptereleotris*	*Parioglossus*
Process on anguloarticular	small	large	absent	absent	absent (rudimentary in *P. palustris*)
Anterior zygapophyses (11)	vertebrae 2-5	vertebrae 2-4	vertebrae 2-4	vertebrae 2-5 (2-11 in *P. monoptera*)	prominent on all precaudal and most caudal vertebrae
Palatopterygoid strut (5)	about 45°	about 45°	almost vertical	almost vertical	almost vertical
Lacrimal (4)	+	−	+	+	reduced
Scapula (2)	well ossified	mostly cartilage	well ossified	mostly cartilage	mostly cartilage
Ventral postcleithrum	+	±	−	+	+
Articular process of premaxilla (6)	shorter than ascending	shorter than ascending	subequal to ascending	subequal to ascending	subequal to ascending
Frontal (13)	not prominent	not prominent	strongly prominent	not prominent	not prominent

Table 3. Frequency distributions of dorsal- and anal-fin counts for species of Aioliops (* indicates holotype count).

Species	First Dorsal Fin			Second Dorsal Fin			Anal Fin	
	IV	V	VI	I,9	I,10	I,9	I,10	I,11
A. brachypterus	1	7*		4	4*		3	5*
A. megastigma			31*	7	24*	4	26*	1
A. novaeguineae			32*	27*	6	7	26*	
A. tetrophthalmus			33*	17*	8		23*	

Table 4. Frequency distributions of pectoral-, pelvic-, segmented caudal- and branched caudal-fin ray counts for species of *Aioliops* (* indicates holotype count).

Species	Pectoral Fin					Pelvic Fin			Segmented Caudal Fin	Branched Caudal Fin	
	14	15	16	17	18	I,2	I,3	I,4	9+8	7+5	7+6
A. brachypterus	1	5*	2			.5	7.5*		8*	1	7*
A. megastigma		2*	10	17	2			31*	31*		31*
A. novaeguineae		1	20*	12				33*	33*		33*
A. tetrophthalmus		1	19*	3				33*	33*		33*

Table 5. Frequency distributions of longitudinal- and transverse-scale counts for species of *Aioliops* (* indicates holotype count).

Species	Longitudinal Scales								Transverse Scales			
	37	38	39	40	41	42	43	44	10	11	12	13
A. megastigma	1	1	1	1	2	1	1	2*			8*	3
A. novaeguineae		4	4	3		2*			5	9*		
A. tetrophthalmus		1	7	3*	1	1			10*	7	2	

Table 6. Frequency distributions of circumpeduncle-scale counts and total gill-raker counts on outer face of first arch for species of *Aioliops* (* indicates holotype count).

Species	Circumpeduncle Scales				Gill Rakers			
	12	13	14	15	14	15	16	17
A. brachypterus					4			
A. megastigma	3*	7	2		2	5	2*	2
A. novaeguineae		6*	3		2	1	5*	
A. tetrophthalmus	1	5	8	4*		12*	2	

Table 7. Measurements of the holotypes of *Aioliops* species (in mm).

Character	*A. brachypterus*	*A. megastigma*	*A. novaeguineae*	*A. tetrophthalmus*
Sex	♂	♀	♀	♂
Standard length	19.0	23.7	18.5	18.4
Head length	5.3	5.7	4.8	4.9
Head width	2.6	3.2	2.7	2.6
Predorsal length	6.6	7.3	6.2	6.3
Body depth	2.7	3.4	2.9	3.1
Mouth	1.7	2.1	1.5	1.8
Eye	1.9	2.1	1.6	1.8
Snout	.9	.8	.7	.6
Caudal-peduncle length	3.9	4.9	4.4	4.3
Caudal-peduncle depth	2.0	2.3	2.1	2.2
Pectoral-fin length	3.7	4.5	4.2	4.2
Pelvic-fin length	3.0	3.7	3.3	3.5
Caudal-fin length	3.6	4.4	3.5	3.8
Third dorsal spine length	1.6	2.0	1.6	1.7
Stripe depth	.7	.7	.4	.5
Caudal-fin spot length	1.8	2.1	1.7	1.8
Preopercular pores	2	3	3	3

Table 8. Standard lengths (mm) and morphometric proportions (percent of SL) for species of *Aioliops*. Morphometric proportions for Timor Sea specimens of *A. novaeguineae* are included in ranges except for stripe depth and caudal-fin spot length where they are placed in parentheses.

Character	*A. brachypterus*	*A. megastigma*	*A. novaeguineae*	*A.tetrophthalmus*
Number examined	8	20	29	33
Standard length (SL)	16.7-19.9	15.9-23.7	12.7-19.5	9.6-22.2
(mean length)	(18.8)	(18.5)	(16.7)	(16.7)
Head length	24.5-27.8	24.1-28.7	24.4-29.3	24.1-30.9
Head width	13.0-14.7	12.5-16.0	11.2-16.0	11.3-18.5
Predorsal length	34.7-36.0	30.8-36.8	31.8-36.4	31.2-38.1
Body depth	14.2-15.8	14.3-19.2	14.9-18.2	14.7-19.7
Mouth	7.8-9.1	7.9-10.5	8.0-10.9	7.2-11.3
Eye	8.4-10.6	8.3-10.7	8.7-10.9	8.8-11.5
Snout	4.0-5.9	3.0-4.3	2.8-4.3	2.8-4.5
Caudal-peduncle length	18.9-20.8	20.6-25.6	21.0-25.6	22.1-27.9
Caudal-peduncle depth	10.5-11.2	9.5-13.5	9.1-13.0	9.2-13.6
Pectoral-fin length	17.0-20.8	17.8-22.8	18.8-23.6	18.1-24.2
Pelvic-fin length				
(males)	14.3-14.9	16.4-20.6	19.0-21.5	16.8-20.8
(females)	12.5-14.2	15.6-19.8	15.9-19.1	15.3-21.0
Caudal-fin length	17.3-20.8	18.6-24.3	19.0-23.5	19.6-24.0
Third dorsal spine length	6.2-8.4	8.3-12.1	8.2-12.5	7.0-12.1
Stripe depth (males)	3.7	2.4-3.8	1.6-2.0 (1.4)	1.9-2.7
(females)	1.5-2.1	1.5-3.1	1.3-2.3 (1.2)	1.6-2.7
Caudal-fin spot length (males)	9.5-10.7	9.6-14.5	9.4-13.8 (12.2)	7.1-12.1
(females)	9.5-9.8	8.3-11.9	9.2-13.0 (10.2)	7.2-10.4
Preopercular pores	2	3	3	3

Aioliops n. gen.

Type species. *Aioliops tetrophthalmus* n. sp., Great Barrier Reef, Queensland, Australia.

Diagnosis. Dorsal fins IV–VI (usually V–VI) + I, 9–10; anal fin I, 9–11; pectoral fins 14–18; pelvic fins separate, I, 3–4; segmented caudal fin 9 + 8; branched caudal fin usually 7 + 6; total gill rakers on outer face of first gill arch, 14–17, compressed and elongate; vertebrae 10 + 16; branchiostegals 5. Head and body compressed; body elongate; ventral and dorsal profiles straight; mouth terminal, oblique; maxilla reaching posteriorly to a point below anterior to middle of pupil; upper jaw slightly protrusible; snout short, round to truncate in side view, less than eye diameter; anterior nostril a short tube or a simple pore; posterior nostril a simple pore; vomer, tongue, and palatines edentate; upper and lower jaws with conical, recurved teeth in 2

rows anteriorly, outer teeth larger than inner; outer anterior teeth of lower jaw directed outward; posteriorly, teeth in 1 or 2 rows; tongue tip round to truncate, tip free from floor of mouth; interorbital about equal to eye diameter; head papillae present, slight variation in number of papillae within and between species (Figs 1, 2); all head pores paired, 7 or 8 on each side of head: posterior nostril pore, interorbital pore, supraocular pore, infraorbital pore, terminal lateral canal pore, 2–3 preopercular pores; gill membrane attached to isthmus below posterior preopercular margin or beneath anterior third of operculum. Head naked; body scales present or absent, when present, mostly ctenoid, 37–44 in longitudinal series; scales on body present from just posterior to pectoral-fin base to caudal fin with 2 rows on caudal fin; posterior scales large; scales beneath first dorsal fin smaller, frequently cycloid; scales absent dorsal to a straight line from spine of second dorsal fin to pectoral-fin base origin; scales on lateral and ventral area of belly cycloid; scales absent from pectoral-fin base and prepelvic area. Caudal fin slightly emarginate.

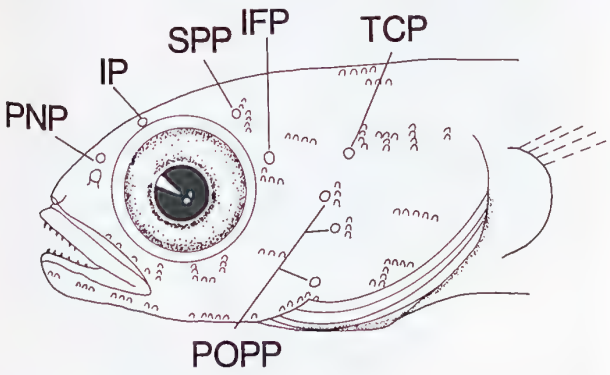

Fig. 1. Head papillae pattern for *Aioliops tetrophthalmus* and head pore terminology for *Aioliops* species. **IFP**, infraorbital pore; **IP**, interorbital pore; **POPP**, preopercular pore; **PNP**, posterior nostril pore; **SPP**, supraocular pore; **TCP**, terminal lateral canal pore.

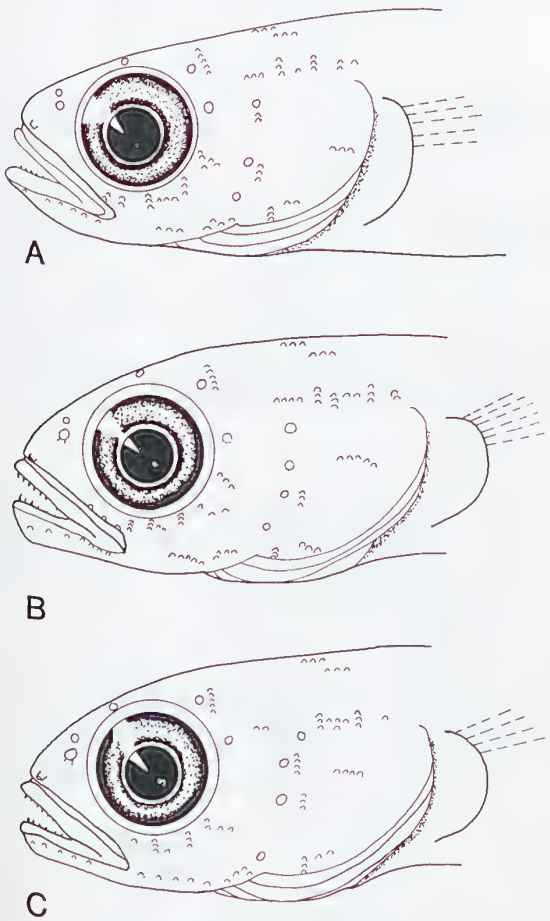

Fig. 2. Head papillae patterns showing slight variations in: **A**, *Aioliops brachypterus;* **B**, *A. megastigma;* and **C**, *A. novaeguineae.*

Osteology. JAWS AND PALATINE BONES (Fig. 3). Premaxillary (PMX) with short ascending process (ASC PMX); articular process of premaxilla (AR PMX) fused with ascending process; postmaxillary process (PM PMX) low; maxillary shaft (MX) slender; dentary (D) with a large, round, coronoid process (COR D);

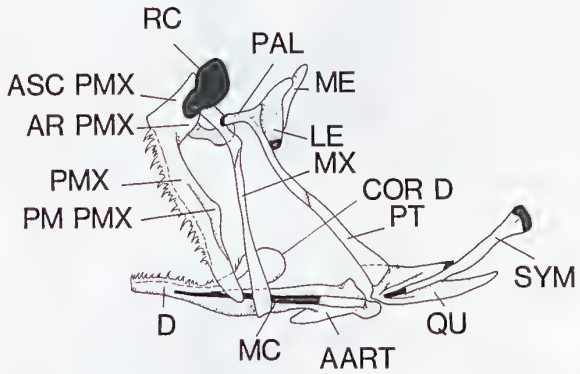

Fig. 3. Jaws and palatine bones of *Aioliops novaeguineae* (left lateral view). Cartilage is shown in black.

anguloarticular (AART) with long, slender, dorsal ramus and short, stout, ventral ramus; prominent dorsolateral process near posterior end of anguloarticular to which tendons from adductor mandibulae attach; retroarticular present; Meckel's cartilage (MC) slender, running along dorsal ramus of anguloarticular; rostral cartilage (RC) large, strongly bound to premaxillae; nasal bone absent; palatine (PAL) L-shaped, articulating with lateral ethmoid (LE); anterior tip of palatine cartilaginous, ectopterygoid (PT) slender.

HYOMANDIBULAR ARCH AND OPERCULAR BONES (Fig. 4). Quadrate (QU) fan-shaped anteriorly with tapered arm posteriorly; symplectic (SYM) slender, laterally expanded at its posterior end, anterior end with cartilage; metapterygoid (MPT) short, slender; no endopterygoid; hyomandibula (HYO) with 3 struts, these articulating with sphenotic, pterotic and operculum; hyomandibula joins metapterygoid

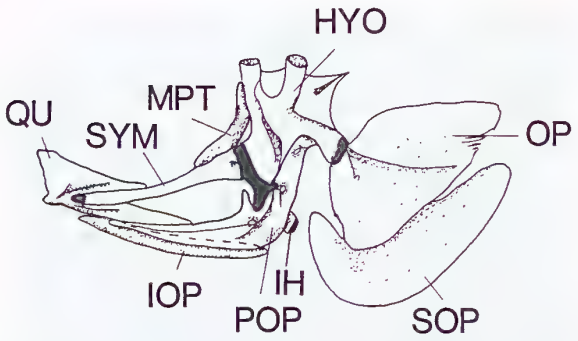

Fig. 4. Hyomandibular arch and opercular bones of *Aioliops novaeguineae* (left lateral view). Cartilage is shown in black.

anteriorly and preoperculum posterolaterally; hyomandibula joined to symplectic by cartilage; 3–5 pseudobranchs present; preoperculum (POP) crescentic with slender, slightly flattened process at inner face of angle, not reaching symplectic; interoperculum (IOP) slender; operculum (OP) triangular; suboperculum (SOP) J-shaped.

Cranial Bones (Fig. 5). Lacrimal absent; lateral ethmoid (LE) fan-shaped, ventral edge cartilaginous; median ethmoid (ME) large, overlapped by frontals; vomer (V) toothless, flattened dorsoventrally; vomer and anterior part of parasphenoid (PS) overlain with ethmoid cartilage; ring of cartilage around eye; dorsal flange of sphenotic (SPH) separated by thin line of cartilage from supraoccipital (SOC); sphenotic

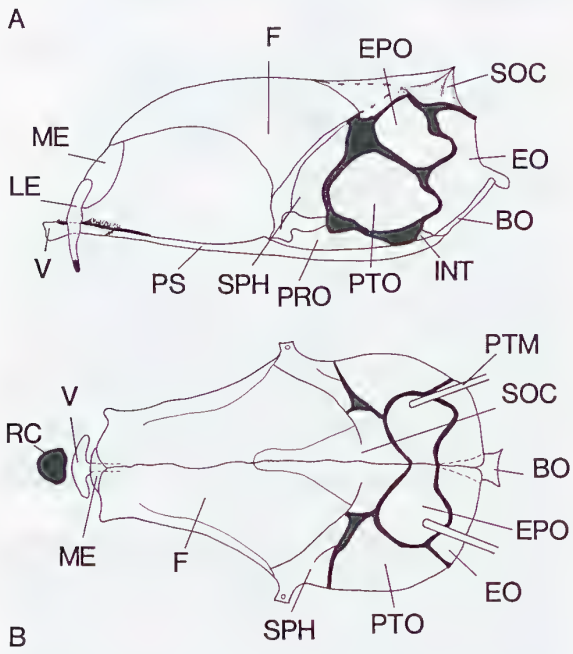

Fig. 5. Cranial bones of *Aioliops novaeguineae*. **A**, left lateral view; **B**, dorsal view. Cartilage is shown in black.

separated from pteroic (PTO) and epioccipital (EPO) by cartilage; proximal end of sphenotic with foramen; supraoccipital (SOC) diamond-shaped with prominent sagittal crest along midline; supraoccipital ridge separates epioccipitals; exoccipitals (EO) overlapped by supraoccipital along most of dorsal midline; exoccipital condyles present; basioccipital (BO) small, Y-shaped; frontal (F) large; subtemporal fossa present, bounded by prootic (PRO), exoccipital, intercalar (INT) and pterotic.

Hyal Bones (Fig. 6). Dorsal and ventral hypohyal (DH, VH) present; anterior ceratohyal (ACH) slender anteriorly, rectangular posteriorly; 5 branchiostegals; first branchiostegal (B1) off slender portion of anterior ceratohyal; branchiostegals 2–4 (B2–4) off rectangular

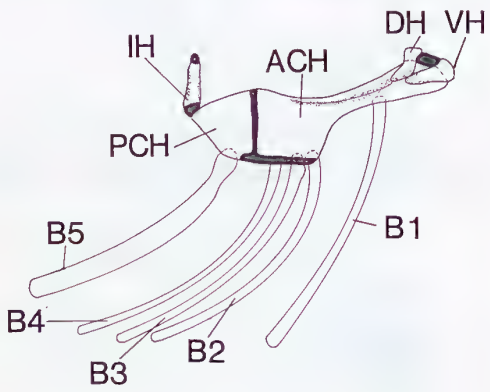

Fig. 6. Hyal bones of *Aioliops novaeguineae* (left medial view). Cartilage is shown in black.

portion of anterior ceratohyal; branchiostegal 5 (B5) off triangular-shaped posterior ceratohyal (PCH); portion of ventral edge of ceratohyal and epihyal cartilaginous; interhyal (IH) cylindrical, cartilaginous at both ends, articulating with posterior ceratohyal ventrally and hyomandibula dorsally, and in contact with preoperculum.

Hyal Bones and Branchial Arch (Fig. 7). Basihyal (BH) spatulate, anteriorly tipped with cartilage; urohyal laterally compressed with dorsal knob connecting to basibranchial 1 (BB1); basibranchial 1 cartilaginous; basibranchial 2 (BB2) slender, posteriorly expanded, both ends with cartilage; basibranchial 3 (BB3) long, slender, both ends tipped with cartilage; basibranchial 4 (BB4) cartilaginous; hypobranchial 1 (HB1) with outer lateral process and cartilaginous at both ends; ceratobranchial 1 (CB1) with cartilaginous tips, 11–13 long, slender ossified gillrakers (GR) along outer edge, approximately 10 pairs long, slender, cartilaginous gill filaments (GF) along median edge; inner edge with 9–10 ossified toothpatches (TP) each bearing 4–5 short, slender teeth; epibranchial 1 (EB1) bifid, each arm with a cartilaginous extension; anterior arm of epibranchial 1 long and slender with 3–4 gill rakers on ossified part of arm and 1 on cartilaginous

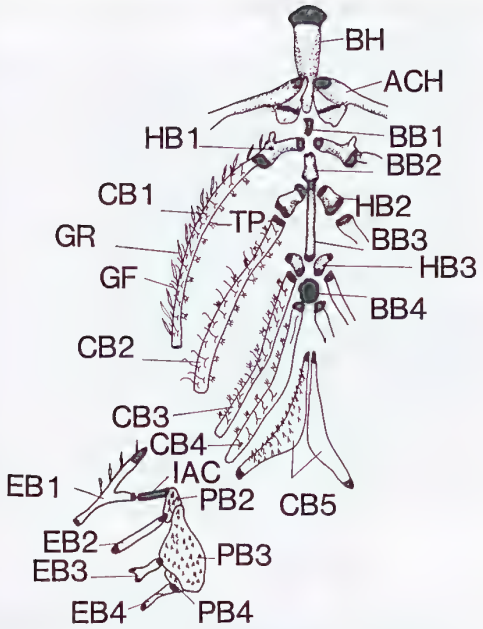

Fig. 7. Hyal bones and branchial arch of *Aioliops novaeguineae* (ventral view). Cartilage is shown in black.

extension; posterior arm connecting with long, slender interarcual cartilage (IAC); hypobranchial 2–3 (HB2–3) with cartilaginous tips; ceratobranchial 2–4 (CB2–4) with ossified toothpatches on sides; cartilaginous gill filaments on median edge; anteriorly epibranchials 2–4 (EB2–4) articulate with their respective infrapharyngobranchials (PB2–4); ceratobranchials 5 (CB5) contiguous but not fused, tipped with cartilage at both ends.

Pectoral Girdle and Pelvic Fins (Figs 8, 9). Posttemporal (PTM) forked, dorsal arm connected to epioccipital, lower arm to intercalar; posteriorly, posttemporal joined to supracleithrum (SCL); cleithrum (CL) bifid dorsally; dorsal postcleithrum absent; ventral postcleithrum absent in *A. brachypterus,* present but small in *A. megastigma, A. novaeguineae* and *A. tetrophthalmus;* paired cleithra joined ventrally, ventral intercleithral cartilage (VICC) present; scapula (SCA) unossified or ossification dorsally above foramen only; large foramen present dorsally in cartilaginous area; coracoid (COR) completely ossified except at attachments to scapula and cleithrum; 4 proximal radials (PRAD); cartilage surrounding posterior margins, anterior margins of ventral 3 radials and anterior and posterior junctions between radials; usually 15–17 cartilaginous distal radials (DRAD) each associated with a pectoral-fin ray; pelvic bone (PL) conical, anteriorly joined by pelvic intercleithral

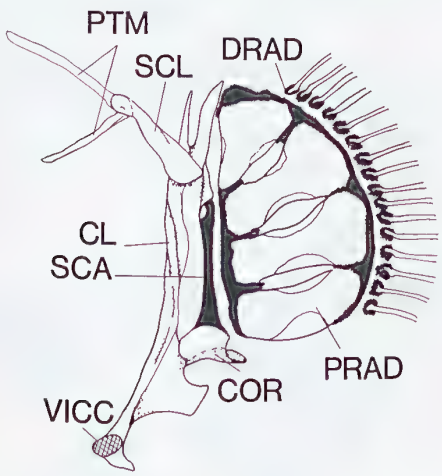

Fig. 8. Pectoral girdle of *Aioliops novaeguineae* (left side). Cartilage is shown in black. Cross-hatching indicates cartilage on underside of bone.

Fig. 9. Pelvic fins of *Aioliops novaeguineae* (ventral view). Cartilage is shown in black.

produced into slender projections extending well beyond fin-ray attachments; ventromedially pelvics bear long, slender anteriorly directed processes which diverge from each other or remain contiguous; posteriorly, pelvics bear 1 spine and 3 or 4 rays attached by cartilage; spine with dorsal, ventral and medial processes connecting it to pelvic; spine and rays in alignment.

Vertebral Column and Median Fins (terminology from Springer, 1983 and Birdsong, 1975). Two pterygiophores between neural spines 3 and 4, 2 between neural spines 4 and 5, 1 between neural spines 5 and 6, 1 between neural spines 6 and 7 [3(22110)] (see comments for *A. brachypterus);* dorsal-fin pterygiophores slender with ventral and posterior

cartilaginous tips; proximal and medial radials of first 2 pterygiophores of second dorsal fin fused; tips cartilaginous; remainder of rays with proximal and medial radials separated with cartilage; spine and all rays except last with partially ossified distal radials; distal radial on last ray absent; first anal-fin pterygiophore precedes first hemal spine; proximal and medial radials of first anal pterygiophore fused; pterygiophore 1 supports anal spine and first ray; second through penultimate pterygiophores with proximal medial and distal radials, each tipped with cartilage; last pterygiophore with no distal radial; vertebral column with 10 precaudal and 16 caudal vertebrae; precaudal vertebrae and occasionally anterior caudal vertebrae

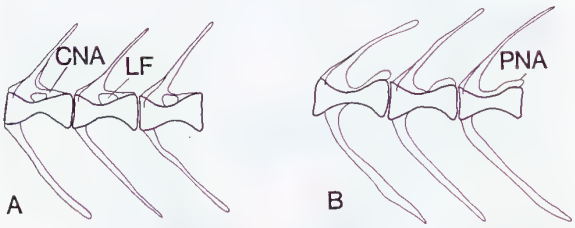

Fig. 10. Caudal vertebrae of: **A,** *Aioliops brachypterus* showing closed neural arch and lateral foramen and **B,** *A. novaeguineae* showing open neural arch and slightly elevated posterior section.

with epipleural ribs becoming progressively further from pleural ribs posteriorly; vertebrae 2–10 with pleural ribs; vertebrae 2–4 with anterior zygapophyses; vertebrae 1–4 or 5 with sides of neural arch usually closed by a process extending from above base of neural spine to posterior end of centrum, lateral foramen present; vertebrae 5–6 to 8–9 with neural arch usually closed, posterior and central sections reduced, foramen present; vertebrae 9–10 to 22, neural arch open, no foramen, posterior section (PNA) usually slightly elevated (Fig. 10B), except for *A. brachypterus* which has closed neural arches (CNA) with lateral foramen (LF) present on vertebrae 9–20 but with low central and posterior sections (Fig. 10A), and vertebrae 21–22 with no central or posterior section and no foramen; neural spines arising from anterior part of centrum on vertebrae 1–20, from anterior to middle part on vertebrae 21–23, and from posterior part on vertebrae 24–25; precaudal vertebrae with parapophyses becoming progressively larger posteriorly; hemal and neural spines of penultimate vertebra broad.

CAUDAL FIN (Fig. 11). Lower hypural plate (LHP) with anteroventral flange; urostyle (US) fused with upper hypural plate (UHP) in all species; urostyle fused with lower hypural plate of *A. novaeguineae* and articulates with lower hypural plate of *A. brachypterus, A. megastigma* and *A. tetrophthalmus;* hypural 5 (HYP 5) slender; one large epural (EPU) present, composed of cylindrical strut and anterior flange; parhypural (PHYP) with anterior flange; neural spine (NS) broad proximally, blade-like distally; dorsal and ventral procurrent cartilage (DPC,VPC) present, each with 7–8 procurrent rays; upper hypural plate with 7 branched rays, uppermost sometimes displaced slightly above plate; lower hypural plate with 6 branched rays, lowermost sometimes displaced slightly below plate; hypural 5, parhypural, last hemal spine (HS) and epural each with one simple, segmented ray.

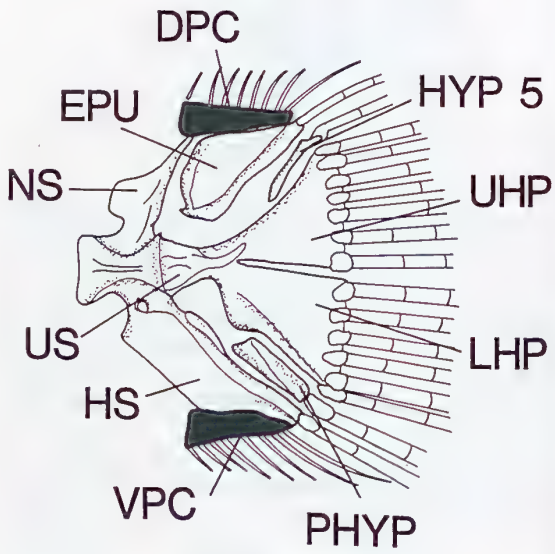

Fig. 11. Caudal fin of *Aioliops novaeguineae* showing urostyle fused with lower hypural plate (left side). Cartilage is shown in black.

Etymology. From the Greek *aiolos* = swift, God of the Wind, and *iops* (masculine) = small fish, named for the speed with which this small fish avoids capture.

Key to Species of *Aioliops*

1. Scales present on body; 3 preopercular pores; usually 6 dorsal spines; pelvic fins I, 4; gill membrane attachment below posterior preopercular margin. 2

——No scales on body; 2 preopercular pores; usually 5 dorsal spines; pelvic fins I, 3; gill membrane attachment behind posterior preopercular margin. .. .. *A. brachypterus*

2. Second dorsal fin usually I, 9; transverse scales usually 10–11; brown stripe on and to either side of ventral midline; anterior edge of caudal-fin spot

extending onto caudal-fin scales in both sexes and may extend onto caudal peduncle. 3

——Second dorsal fin usually I, 10; transverse scales 12–13; no brown stripe on and to either side of ventral midline; anterior edge of caudal-fin spot not extending onto caudal-fin scales although males may have lighter speckling anterior to main spot which extends onto caudal-fin scales. ..... *A. megastigma*

3. Pelvic-fin rays of males usually extending to anus; caudal-fin spot extending onto caudal peduncle ventral to midline; scattered brown speckling usually present on dorsal midline anterior to caudal peduncle; lateral stripe extending onto dorsal caudal-fin rays. ..... *A. novaeguineae*

——Pelvic-fin rays of males not extending to anus; caudal-fin spot not extending onto caudal peduncle, usually extending onto last row of caudal-fin scales; scattered brown speckling rarely present on dorsal midline anterior to caudal peduncle; lateral stripe not extending onto dorsal caudal-fin rays. ... *A. tetrophthalmus*

Aioliops brachypterus n.sp.

Figs 12, 16

Type material. HOLOTYPE: NSMT P.44087, Mini Rock Island, El Nido Island, Philippines, 5 June 1984, ♂, 19.0 mm. PARATYPES: LICPP 1984275, taken with holotype, 7(17–20 mm).

Diagnosis. (Based on 8 specimens, 2 ♂ and 6 ♀, from one sample.) Dorsal fins IV–V (usually V) + I, 9–10; anal fin I, 10–11; pectoral fins 14–16; pelvic fins I, 3 (one specimen with I, 2 on one side only), all segmented rays unbranched; scales absent; anterior nostril a simple pore; 2 preopercular pores, other pores as for genus; posterior teeth of both jaws in one row; gill membrane attaching to isthmus beneath anterior third of operculum; snout long (4.0–5.9% of SL); caudal peduncle length short (18.9–20.8% of SL); first dorsal fin short (length of third dorsal spine 6.2–8.4% of SL); pelvic fin short (12.5–14.9% of SL); caudal fin short (17.3–20.8% of SL); males with predorsal area dark; females with dorsolateral stripe commencing above or behind posterior preopercular margin; dark stripe, on and to either side of ventral midline posterior to anus; roundish spot on caudal fin, spot extending onto ventral portion of caudal peduncle; ventral postcleithrum absent; vertebrae 10–20 with neural arches closed and foramen present.

Description. Snout round to truncate in side view, 1.8–2.1 in eye; gill rakers on outer face of first arch 3 + 1 + 10 (= 14). First dorsal fin originating about eye diameter or slightly more than eye diameter posterior to pectoral-fin base origin; no elongate or filamentous dorsal spines, spine 2 longest, slightly longer than 3, spines 1 and 4 about equal, less than 2 and 3, spine 5 shortest; dorsal and anal segmented rays 2 and 3 longest, posterior segmented rays decreasing in length to last ray; first dorsal- and anal-fin segmented ray unbranched, other rays branched; pectoral fins with round margin; second segmented pelvic ray longest.

Colour in alcohol. Body yellow; males with top of head from first dorsal fin to tip of upper lip dark; females with sparse to dense patch of brown chromatophores across head from just posterior to eye to over posterior portion of operculum and with small patch of round, brown chromatophores just ventral to infraorbital pore; males with brown patch extending from infraorbital pore posteriorly over dorsal portions of preoperculum and operculum and with brown speckling on tip of lower lip, suborbital, and dorsal and ventral edges of pectoral-fin base; both sexes with brown chromatophores on bases of pectoral-fin rays, and

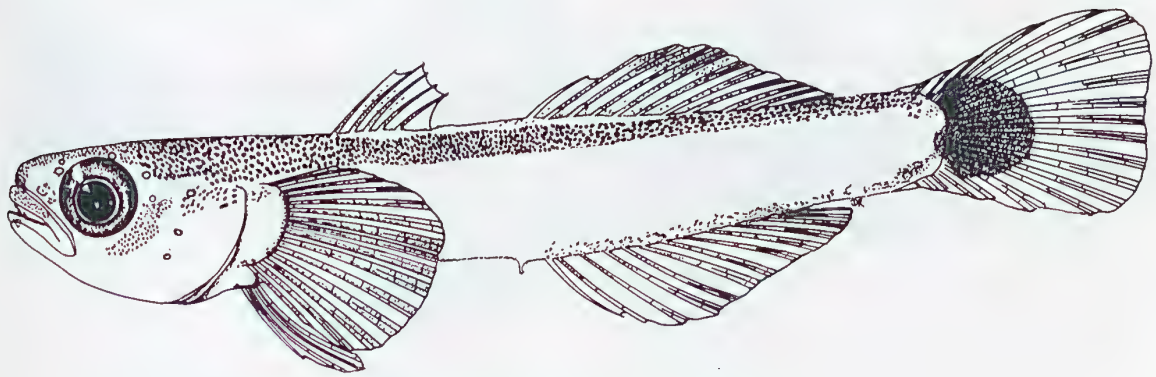

Fig. 12. Holotype of *Aioliops brachypterus*, Philippines, ♂, 19.0 mm (NSMT P.44087).

occasionally pelvic-fin base and rays; females with subdermal brown stripe on lateral portion of gut, males with subdermal pigmentation on most of gut; males with several brown chromatophores scattered anteriorly on lateral portion of trunk (obscured by pectoral fin); females with brown speckling on belly; sparse brown speckling at base of dorsal fins; dorsolateral stripe of males commencing beneath first dorsal fin, stripe of females beginning above posterior preopercular margin to middle of opercular margin; stripe extending along trunk and tail to upper edge of caudal peduncle where both sides of stripe are connected by randomly scattered chromatophores across dorsal midline; lateral stripe deeper in males than females, stripe below first dorsal fin 1.2–1.3 in pupil diameter for males, 1.6–2.0 in pupil diameter for females; both sexes with speckling on and to either side of ventral midline from anus to caudal peduncle; roundish black spot on caudal fin, ventral half of spot extending onto caudal peduncle; spot partially covering rays 2–3 to 16–17; average number of partially pigmented caudal-fin rays, 14; spot length about equal to eye diameter; dorsal, anal and pectoral fins lightly spotted; pelvic fins pale.

Distribution. Mini Rock Island, El Nido Island, the Philippines.

Etymology. From the Greek *brachy* = short and *pteron* = fin, named for the relatively short lengths of the dorsal, caudal and pelvic fins.

Comments. Although the ventral half of the caudal-fin spot extends onto the caudal peduncle of both *A. brachypterus* and *A. novaeguineae* the lack of scales, 5 dorsal spines, 3 ventral rays which are all unbranched, more restricted gill opening and 2 preopercular pores easily distinguish *A. brachypterus* from the other three species. *Aioliops brachypterus* is also distinctive in the genus in having a longer snout, shorter caudal peduncle length, shorter pelvic-fin length, shorter caudal-fin length, shorter first dorsal-fin height, significantly lower pectoral-fin ray counts ($p<0.001$) and significantly higher anal fin-ray counts ($p<0.01$) compared to the other species. The depth of the lateral stripe beneath the first dorsal fin of the males is larger than those of *A. novaeguineae* and *A. tetrophthalmus* but approximately equal to that of *A. megastigma*.

The densely pigmented predorsal region of the male is the most obvious colour difference separating *A. brachypterus* from the other species. However, more subtle differences are present such as the higher number of partially pigmented caudal-fin rays (average of 14 for *A. brachypterus* and 7.5–10 for the other species) and the point of origin of the female lateral stripe which is over or behind the posterior preopercular margin in *A. brachypterus*.

The absence of the ventral postcleithrum distinguishes this species osteologically from the other species. Although *A. brachypterus* has only 5 dorsal spines, the one cleared and stained specimen has 6 pterygiophores associated with the first dorsal fin. Of the radiographs taken, one shows a faint spot where the sixth pterygiophore would normally occur while the quality of the other 6 radiographs are too poor to determine if the pterygiophore is present. On the basis of its presence in the cleared and stained specimen, it is assumed that the pterygiophore formula is normally 3(22110).

Within the species there is sexual dimorphism. The pelvic fins are longer and the lateral stripe is deeper in males. Both sexes are pigmented in similar areas, however, males have a much higher concentration of spots on the predorsal region.

One of the 8 specimens is unique in having a first dorsal fin of 4 spines and pelvic fins with counts of I, 2/I, 3. As this was the only specimen found with lower counts, it is presumed to be atypical.

Aioliops megastigma n.sp.

Figs 13, 16

Type material. HOLOTYPE: NSMT-P.44114 El Nido Island, Philippines, 6–25 March 1983, ♀, 23.7 mm. PARATYPES: AMS I.25434-001, north of Lesser Mendjangan Island, Karimundjawa Islands, Indonesia, 5°53′S 110°25′E, V. Springer & M. Gomon, 30 May 1974, 2(19–20 mm); AMS I.25435-001, Bararin Island, Palawan Province, Philippines,

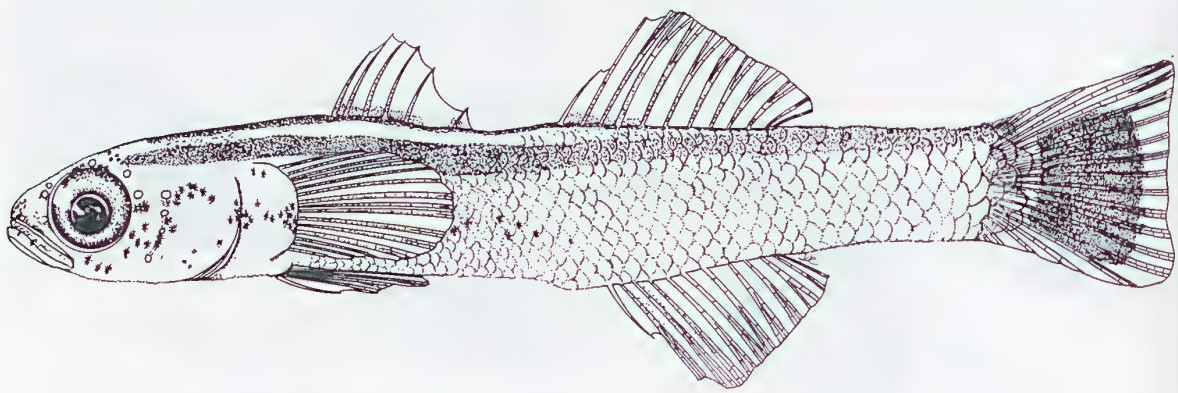

Fig. 13. Holotype of *Aioliops megastigma*, Philippines, ♀, 23.7 mm (NSMT P.44114).

10°53′N 120°56′E, 0–15 m, Smithsonian team, 23 May 1978, 2(16–17 mm), cleared and stained 1(16 mm); CAS 57923 same data as I.25435-001 1(18 mm); LICPP 1984269, Mini Rock Island, El Nido Island, Philippines, 5 June 1984, 4(16–20 mm); USNM 246731, same data as AMS I.25434-001, 8(18–20 mm); USNM 257044, south-west coast of Karimundjawa Island, Indonesia, 5°53′S 110°26′E, 1–13 m, V. Springer, 29 March 1974, 3(16–18 mm); USNM 257054, same data as AMS I.25435-001, 11(16–18 mm).

Diagnosis. Dorsal fins VI + I, 9–10 (usually I, 10); anal fin I, 9–11 (usually I, 10); pectoral fins 15–18; pelvic fins I, 4; scales present, 37–44 in longitudinal series, 12–13 in transverse series; anterior nostril a short tube; 3 preopercular pores, other pores as for genus; posterior teeth of both jaws in one row; gill membrane attached to isthmus below posterior margin of preoperculum; dark stripe on dorsal midline; depth of male lateral stripe 2.4–3.8% of SL; round to oblong spot on caudal fin beginning about pupil diameter posterior to caudal peduncle.

Description. Snout round in side view, 2.0–3.2 in eye; gill rakers of first gill arch 3–4 + 1 + 10–13 (= 14–17). First dorsal fin originating about eye diameter or slightly more than eye diameter posterior to pectoral-fin base origin; no elongate or filamentous dorsal spines; spines 2–3 about equal in length, spine 4 slightly shorter, spines 1 and 5 about equal in length, shorter than 2–4, spine 6 shortest; dorsal and anal segmented rays 2 and 3 longest, posterior rays decreasing slightly in length to last ray; all dorsal and anal segmented rays branched except first dorsal segmented ray which is unbranched; pectoral fins oblong; pelvic fins not reaching to anus in either sex; pelvic ray 3 longest; innermost pelvic ray unbranched, others branched.

Colour of fresh material. Background colour whitish; snout, preoperculum and operculum yellowish grey; dark brown, lateral stripe along dorsolateral portion of body originating just posterior to supraocular pore and continuing to end of caudal peduncle; dark brown stripe along dorsal midline from nape to end of caudal peduncle; large, dark brown, vertically oblong spot on caudal fin beginning about pupil diameter posterior to caudal peduncle; belly bright blue; wide yellowish orange stripe along ventral midline from beginning of anal fin to end of caudal peduncle and extending onto lower third of body; fins clear.

Colour in alcohol. Background colour of body and head yellow; snout, upper lip and tip of lower jaw with small brown chromatophores slightly speckled in females, moderately speckled in males; small, brown chromatophores on throat, suborbital, preoperculum, upper portion of operculum, pectoral-fin base, and occasionally just dorsal to pectoral-fin base in both sexes, denser in males than females, and occasionally absent in one or more of these locations in females; males with brown speckling on anterior portion of branchiostegal membrane, prepelvic area, and frequently pelvic-fin base and anterior portion of pelvic rays; brown speckling across posterior portion of interorbital in males and on head just posterior to eyes in both sexes; occasionally entire head of males covered in moderately spaced, round, brown chromatophores; brown, subdermal chromatophores on lateral portion of gut in both sexes; males with brown chromatophores at base of urogenital papilla and randomly scattered on belly; both sexes with several brown chromatophores along lateral area of trunk, denser in males than females and frequently absent in females; chromatophores occasionally extending along tail of males and forming dense patch on lateral midline just anterior to caudal fin; narrow brown stripe along dorsal midline from just posterior to eye and continuing to end of second dorsal fin; random speckling on midline posterior to second dorsal fin; dark brown stripe commencing just posterior to supraocular pore in females and just anterior to supraocular pore in males, continuing along dorsolateral portion of body and terminating on anterior portion of dorsal caudal-fin rays; depth of lateral stripe below first dorsal fin approximately equal to pupil diameter; large, brown to black, round to oblong spot on caudal fin usually occurring on rays 2–5 to 13–17 in males and 4–6 to 12–15 in females, but may cover part of all segmented rays; average number of partially pigmented caudal-fin rays, 10; spot length equal to or greater than eye diameter in females, greater than eye diameter in males; anterior edge of spot about a pupil's diameter posterior to end of caudal peduncle; males with mid-anterior portion of spot occasionally lighter and extending onto caudal peduncle; males with proximal quarter of dorsal fins dark; dorsal fins of females and anal and pectoral fins of both sexes lightly speckled; pelvic fins whitish.

Distribution. Indonesia (excluding Irian Jaya) and the Philippines.

Etymology. From the Greek *mega* = large and *stigma* = spot, named for the large caudal-fin spot, and treated as a noun in apposition.

Comments. *Aioliops megastigma* is separated geographically from *A. novaeguineae* and *A. tetrophthalmus,* but has been collected from the Philippines with *A. brachypterus.* This species, however, is readily distinguished from *A. megastigma* by the absence of scales, 2 preopercular pores, 5 dorsal spines and a more restricted gill opening. *Aioliops megastigma* is distinct from *A. novaeguineae* and *A. tetrophthalmus* in having a significantly higher ($p<0.01$) dorsal-fin ray count (usually 10 for *A. megastigma* compared to usually 9 for the other two species) and a significantly higher ($p<0.001$) number of transverse scale rows (12–13 for *A. megastigma* compared to 10–11 (rarely 12) for the other two species). In addition *A. megastigma* has a significantly higher ($p = 0.05$) number of pectoral-fin rays compared to *A. tetrophthalmus* (usually 17 for *A. megastigma,* usually 16 for *A. tetrophthalmus).*

Colour differences may also be used to separate the species. Males of *A. novaeguineae* and *A. tetrophthalmus* have a narrower lateral stripe, a midventral stripe on the tail and a more rounded caudal-fin spot which originates on or anterior to the caudal-

fin scales. The average number of caudal-fin rays partially covered by the spot is higher in *A. megastigma* (10) than in the other two species (7.5, 8.3).

Colour differences between the two sexes are slight. Males are frequently more densely pigmented and usually have a slightly deeper lateral stripe (2.4–3.8% of SL for males, 1.5–3.1% of SL for females) and a slightly larger caudal-fin spot (9.6–14.5% of SL for males, 8.3–11.9% of SL for females) than females.

Aioliops novaeguineae n. sp.

Figs 14, 16

Type material. HOLOTYPE: USNM 276500, Milne Bay, Basilaki Island, Papua New Guinea, 0–3 m, 22 Aug 1975, ♀, 18.5 mm. PARATYPES: AMS I.17089-043, Madang Harbour, Krankett Island, Papua New Guinea, 5°11′S 145°50′E, 2–8 m, coral with sand patches, B. Collette, B. Goldman & G. Palmer, 30 May 1970, 1(16 mm); AMS I.25548-001, collected with holotype, cleared and stained, 2(17–19 mm); USNM 244194, Hawaii Island, Marchesa Bay, Batanta Island, Irian Jaya, Indonesia, 0°50′S 130°57′E, 0–6 m, B. Collette & party, 2 July 1979, 31(12–18 mm), cleared and stained, 4(17–18 mm); USNM 257042, Siar Island, Madang, Papua New Guinea, 0–2 m, W. Ponder & P. Colman, 31 May 1970, 1(15 mm); USNM 257046, Krankett Island, Madang Harbour, Papua New Guinea, 1–8 m, B. Collette, 30 May 1970, 9(12–15 mm); USNM 261548, collected with holotype, 7(11–19 mm).

Other material. AMS I.21316-054, South Reef lagoon, Scott Reef, Timor Sea, 14°10′S 121°55′E, 7–10 m, *Acropora* coral and sand, F. Talbot, 20 Sept 1979, 2(14–17 mm).

Diagnosis. Dorsal fins VI + I, 9–10 (usually I, 9); anal fin I, 9–10 (usually I, 10); pectoral fins 15–17 (usually 16–17); pelvic fins I, 4; scales present, 38–42 in longitudinal series, 10–11 in transverse series; anterior nostril a short tube; 3 preopercular pores, other pores as for genus; posterior teeth in one row; gill membrane attached to isthmus below posterior margin of preoperculum; pelvic fins of males long, reaching to anus (19.0–21.5% of SL); dark stripe present on and to either side of ventral midline posterior to anus; round to oval, black spot on caudal fin, spot extending onto ventral portion of caudal peduncle; urostyle fused with lower hypural plate.

Description. Two specimens collected from the Timor Sea have slight colour differences and may represent a separate species; however due to a lack of material from that locality and the similarities between those specimens and *A. novaeguineae*, they are included in the description of *A. novaeguineae*. Snout round in side view, 2.1–3.7 in eye; gill rakers on outer face of first arch 3 + 1 + 10–12 (=14–16). First dorsal fin originating about eye diameter posterior to pectoral-fin base origin; no elongate or filamentous dorsal spines; spines 2–3 longest and about equal in length, longer than spine 4, spines 1 and 5 about equal in length, shorter than 2–4, spine 6 shortest; dorsal and anal segmented rays 2 and 3 longest, posterior rays decreasing in length to last ray; all dorsal and anal segmented rays branched except first dorsal segmented ray which is unbranched; pectoral fins oblong; pelvic fins not reaching to anus in females; pelvic ray 3 longest; innermost pelvic ray unbranched, others branched.

Colour in alcohol. The following colour description represents all specimens, including those from the Timor Sea unless otherwise stated. Background colour yellow; snout, upper lip and tip of lower lip with small, brown chromatophores; throat frequently spotted in males, occasionally spotted in females; brown, subdermal chromatophores over skull and brown chromatophores on dorsal portion of head just posterior to eye; females with several small chromatophores just ventral and posterior to infraorbital pore and occasionally just posterior to corner of jaw; males usually with small chromatophores just posterior to corner of jaw and lower portion of preoperculum, a series of chromatophores just below infraorbital pore to upper portion of operculum and occasionally with most of preoperculum spotted; males with several chromatophores on anterior portion of branchiostegal membrane, over pectoral-fin base, and just ventral to pectoral-fin base except male from Timor Sea which is unspotted in these areas; subdermal stripe on lateral portion of belly in females, entire belly of males subdermally pigmented; belly of males with small, brown chromatophores; belly of females unspotted; males with several small, brown chromatophores on lateral portion of trunk and occasionally on tail; male from Timor Sea with posterior portion of caudal peduncle with densely spaced, brown chromatophores; females frequently with small dark speckling around anus, males frequently with base of urogenital papilla dark brown; narrow stripe along entire dorsal midline

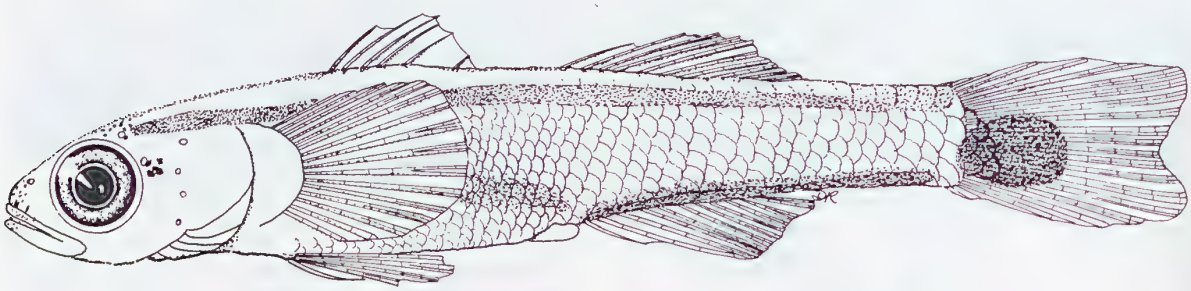

Fig. 14. Holotype of *Aioliops novaeguineae*, Papua New Guinea, ♀, 18.5 mm (USNM 276500).

although spotting occasionally sparse on predorsal area; specimens from Timor Sea without dorsal midline stripe, speckling restricted to base of dorsal fins and on dorsal portion of tail posterior to second dorsal fin; brown to black stripe, depth below first dorsal fin about half pupil diameter (one third pupil diameter for Timor Sea specimens), originating just posterior to supraocular pore and extending along dorsolateral portion of body to caudal peduncle and occasionally extending less densely onto anterior portion of dorsal caudal-fin rays; ventral stripe originating at anus and terminating on caudal peduncle anterior to caudal fin; dark brown, round to oval spot on caudal fin-rays 6–8 to 14–16 for specimens from Papua New Guinea and fin rays 8–9 to 16 for specimens from the Timor Sea; average number of partially pigmented caudal-fin rays, 8.3 (7.5 for Timor Sea specimens) spot extending onto caudal peduncle below lateral midline; spot length equal to or slightly greater than eye diameter; dorsal and pectoral fins lightly spotted; others clear.

Distribution and ecology. Papua New Guinea, Irian Jaya and possibly the Timor Sea; found on coral reef drop-offs from 1–10 m.

Etymology. Named *novaeguineae* for the type locality.

Comments. The fusion of the lower hypural plate to the urostyle distinguishes this species osteologically from the other three species as well as other species in the subfamily. Colour similarities between *A. novaeguineae, A. tetrophthalmus* and females of *A. brachypterus* may cause some confusion when trying to identify the species, however, the following morphometric and meristic characters of *A. novaeguineae* allow easy separation from *A. brachypterus:* ctenoid scales, 3 preopercular pores, anal fin usually I, 9–10, and pelvic fins I, 4. The males of *A. brachypterus* are much more densely pigmented on the head and lateral portions of the body and are not likely to be misidentified. Differences between *A. novaeguineae* and *A. tetrophthalmus* are more subtle, and other than the pelvic fins, which are longer in the males of *A. novaeguineae,* the most prominent distinguishing feature is the caudal-fin spot which does not extend onto the caudal peduncle in *A. tetrophthalmus.* Certain other colour differences occur, but due to fading, preserving techniques or age of the specimens, these differences are often difficult to see. *Aioliops megastigma* can be separated from *A. novaeguineae* by the number of dorsal-fin rays (usually I, 10 for *A. megastigma),* a ventral stripe in *A. novaeguineae* as opposed to no ventral stripe in *A. megastigma,* a stripe depth less than the pupil diameter versus a stripe depth about equal to the pupil diameter in *A. megastigma,* and a caudal-fin spot which originates anteriorly on the caudal peduncle versus a spot which originates about a pupil diameter posterior to the caudal peduncle in *A. megastigma.*

Sexual dimorphism appears to be limited to the length of the pelvic fins (longer in males) and to slight colour variations, with males more densely pigmented than females.

No morphometric or meristic differences are evident between the specimens from Papua New Guinea and those from the Timor Sea other than the depth of the lateral stripe which is deeper in the former and the average number of rays covered by the caudal-fin spot which is less for the two Timor Sea specimens. However, these features could not be considered statistically different from *A. novaeguineae* without examining more material. The pelvic-fin length of *A. novaeguineae* males seems to be unique in the genus in reaching to the anus, and as the pelvic-fin rays of the male collected from the Timor Sea also reach to the anus, the implication is that these are the same species.

The Timor Sea is not separated from the Papua New Guinea region by any land form or deep water body, and it is likely that the range of *A. novaeguineae* extends to the north-eastern Indian Ocean. The area off north-western Australia has not been extensively sampled and any further collecting in the Timor Sea and eastern Indian Ocean should help to resolve the question as to whether a fifth species of *Aioliops* is present.

Aioliops tetrophthalmus n. sp.

Figs 15, 16

Type material. All from Great Barrier Reef, Queensland, Australia. HOLOTYPE: AMS I.22723-008, Mrs Watsons Bay, Lizard Island, 14°40′S 145°27′E, 0–4 m, D. Hoese & party, 15 Sept 1981, ♂, 18.4 mm. PARATYPES: AMS I.18740-120, Yonge Reef, 14°35′S 145°36′E, 14 m, AMS party, 8 Nov 1975, 1(15 mm); AMS I.18755-131, Palfrey Island lagoon, Lizard Island, 14°40′S 145°27′E, 4–8 m, coral and sand, AMS party, 2 Nov 1975, 3(12–18 mm); AMS I.18805-070, 1 mile north of Lizard Island, 14°40′S 145°28′E, sand cay, D. Hoese & H. Larson, 28 Jan 1975, 4(10–15 mm); AMS I.19442-085, North Direction Island, 14°44′S 145°31′E, 12 m, sand and coral, Lizard Island team, 5 Nov 1975, 10(9–15 mm); AMS I.19473-215, Coconut Beach, Lizard Island, 14°40′S 145°27′E, 2–7 m, coral and sand, AMS party, 24 Nov 1975, 1(16 mm); AMS I.20779-140, Tijou Reef, Cape York, 13°05′S 143°57′E, 0–25 m, coral and sand, AMS party, 22 Feb 1979, 3(18–20 mm); AMS I.20956-006, Tijou Reef, Cape York, 13°04′S 143°57′E, 3–12 m, coral bommie, silt and sand, AMS party, 23 Feb 1979, 7(15–18 mm), cleared and stained 2(15–16 mm); AMS I.20994-002, lagoon entrance, Lizard Island, 14°39′S 145°27′E, 2–7 m, coral, sand and rubble, D. Hoese & H. Larson, 11 Dec 1978, 36(8–15 mm), cleared and stained, 3(10–11 mm); AMS I.21539-088, between Bird and South Island, Lizard Island, 14°42′S 145°27′E, 2–8 m, D. Hoese & H. Larson, 8 Feb 1975, 3(11–20 mm), cleared and stained, 2(17–18 mm); AMS I.22581-037, back reef slope, Escape Reef North, 15°49′S 145°50′E, 10–14 m, coral and sand, AMS party, 29 Oct 1981, 3(12–19 mm), cleared and stained, 2(17–19 mm); AMS I.22723-003, collected with holotype, 5(18–22 mm); AMS I.25269-001, North point, Lizard Island, 14°40′S 145°28′E, 5 m, H. Larson, 20 Sept 1981, 4(11–18 mm); ANSP 156917, same data as AMS I.20994-002, 2(12–16 mm); BMNH 1985.7.27.1-2, same data as AMS I.21539-088, 2(15–18 mm); BPBM 30644, same data as AMS I.22581-037, 2(12–16 mm); CAS 57354, south side

of Palfrey Island, Lizard Island lagoon, 14°42′S 145°27′E, 3–10 m, coral, sand and rubble, AMS party, 21 Nov 1975, 3(13–16 mm); NMV A3510, same data as AMS I.22581-037, 2(13–14 mm); NTM S.11674-001, same data as AMS I.20779-140, 2(17–18 mm); QM I.21688, same data as AMS I.20956-006, 2(15–17 mm); USNM 273305, collected with holotype, 2(19–21 mm); WAM P28454-001, Lizard Island, 14°41′S 145°26′E, 1–8 m, D. Hoese & party, 27 Nov 1975, 2(15–20 mm).

Additional material. AMS I.19108-131, Bird Islet, Lizard Island, 1(9 mm) AMS I.19461-078, Decapolis Reef, 1(11 mm).

Diagnosis. Dorsal fins VI + I, 9–10 (usually I, 9); anal fin I, 10; pectoral fins 15–17 (usually 16–17); pelvic fins I, 4; scales present, 38–42 in longitudinal series, 10–12 (usually 10–11) in transverse series, anterior nostril a short tube; 3 preopercular pores, other pores as for genus; posterior teeth of both jaws in 1–2 rows; gill membrane attached to isthmus below posterior margin of preoperculum; dark stripe present on and to either side of ventral midline posterior to anus; round spot on caudal fin, extending anteriorly onto one row of caudal-fin scales.

Description. Snout short (2.3–3.7 in eye), round in side view; gill rakers on outer face of first arch 3 + 1 + 10–12 (= 14–16). First dorsal fin originating about eye diameter posterior to pectoral-fin base origin; no elongate or filamentous dorsal spines; spines 2–3 longest and about equal in length, spines 1 and 5 about equal in length, shorter than 2–4, spine 6 shortest; dorsal and anal segmented rays 2 and 3 longest, posterior rays decreasing in length to last ray; all dorsal and anal segmented rays branched except first dorsal segmented ray which is unbranched; pectoral fins oblong, pelvic ray 3 longest, not reaching to anus in either sex; innermost pelvic ray unbranched, others branched.

Colour of fresh material. Background colour whitish yellow; head with many small, round, black and reddish orange chromatophores; several small black and reddish orange chromatophores on pectoral-fin base and breast; few scattered melanophores on lateral portion of trunk anteriorly; black stripe along dorsolateral portion of body from just posterior to eye to end of caudal peduncle; thin black stripe along ventral midline from anal spine to end of caudal peduncle; anterior half of caudal fin with large round, black spot surrounded dorsally, posteriorly, and ventrally by wide, yellow margin; first dorsal fin with orange stripe across midportion of fin; second dorsal and anal fins with minute white spots, pectoral fins clear; pelvic fins white with broad, transverse, pale brown bands, often broken into irregularly shaped spots.

Colour in alcohol. Specimens less than 15 mm are not as heavily pigmented as larger specimens and may be lacking some of the pigment described below: background colour whitish yellow; snout, upper lip, tip of lower lip and occasionally suborbital, throat and anterior portion of branchiostegal membrane with brown speckling; males with brown pigment on suborbital and throat more often than females; females occasionally with brown patch just ventral to infraorbital pore; males with brown chromatophores on preoperculum and anterior half and occasionally dorsoposterior portion of operculum; males with brown chromatophores on pectoral-fin base and just dorsal to pectoral-fin base, chromatophores occasionally on anterior portion of pectoral-fin rays; dense patch of brown chromatophores on breast of males; scattered brown chromatophores over posterior portion of interorbital although spotting may be confined to sides and absent from midline; males usually with dark belly; belly of females pale; brown subdermal stripe on either side of belly in both sexes, more prominent in females; males frequently with few to many small brown chromatophores randomly scattered over trunk ventral to lateral stripe; females occasionally with narrow brown speckling around anus; brown speckling on dorsal midline at bases of dorsal fins and posterior to second dorsal fin; few spots rarely present on head posterior to skull; lateral stripe commencing from over or just anterior to preoperculum and terminating at end of caudal peduncle; depth of stripe under first dorsal fin less than pupil diameter; ventral midline stripe terminating at or slightly before posterior end of caudal peduncle; large, brown, round spot on caudal fin from rays 5–8 to 13–16; average number of partially pigmented caudal-fin rays, 7.5; anterior edge of spot extending onto one row of caudal-fin scales although light speckling occasionally extends onto caudal

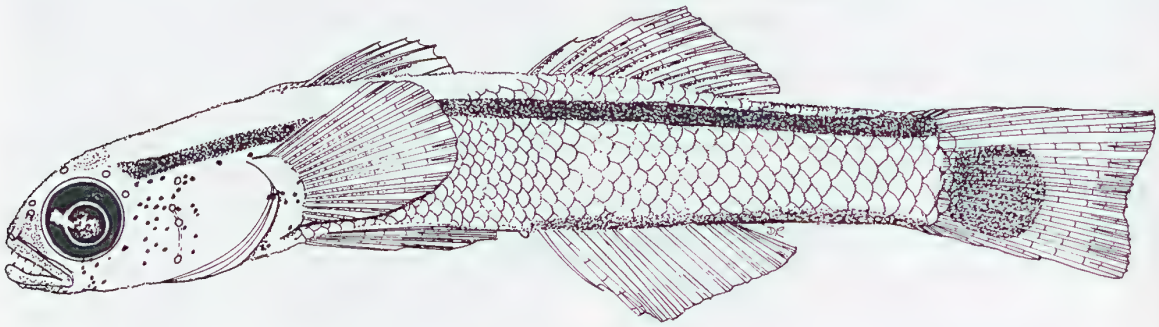

Fig. 15. Holotype of *Aioliops tetrophthalmus*, Lizard Island, Queensland, ♂, 18.4 mm (AMS I. 22723-008).

peduncle; anterior portion of spot originates less than pupil diameter (usually 0.3–0.5 pupil diameter) posterior to caudal peduncle, length of spot about equal to eye diameter; dorsal, anal and pectoral fins lightly spotted; pelvic fins clear.

Distribution and ecology. Tropical eastern Australia; found on coral reef drop-offs from 1–25 m.

Etymology. From the Greek *tetra* = four and *ophthalmus* = eye, named for the four-eyed appearance created by the caudal-fin spot.

Comments. *Aioliops tetrophthalmus* can be distinguished from *A. brachypterus* by the presence of scales, 3 preopercular pores, pelvic fins I, 4 and anal fin usually I, 9–10. It can also be distinguished from *A. megastigma* by a second dorsal fin usually with I, 9 (I, 10 for *A. megastigma),* and 10–11 transverse scales (compared to 12–13).

Aioliops tetrophthalmus is very similar in colouration to *A. novaeguineae* but differs in the anterior origin of the caudal-fin spot which is on the caudal-fin scales in *A. tetrophthalmus* but on the caudal peduncle in *A. novaeguineae.* Several other colour differences exist, such as the posterior extension of the lateral stripe onto the caudal fin in *A. novaeguineae,* but not in *A. tetrophthalmus*, and the average number of pigmented caudal-fin rays (8.3 in *A. novaeguineae* and 7.5 in *A. tetrophthalmus).* However, these colour patterns also vary within each species due to the condition of the specimens and cannot be used as distinguishing features alone.

There appears to be no sexual dimorphism in the

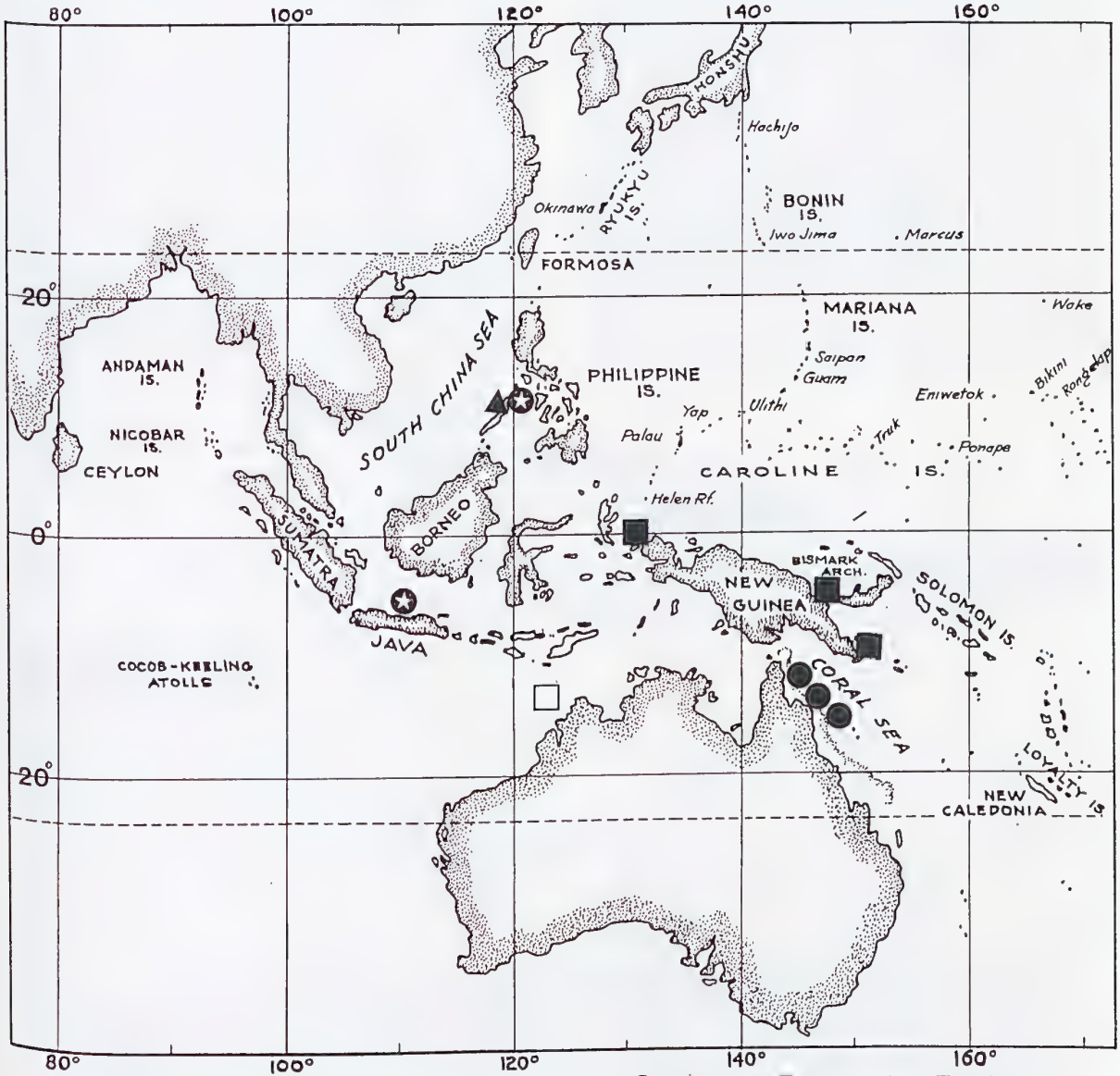

Fig. 16. Geographic distribution of *Aioliops* species: ▲ *A. brachypterus,* ✪ *A. megastigma,* ■ *A. novaeguineae* (□ specimens tentatively identified as *A. novaeguineae)* and ● *A. tetrophthalmus.*

species; colour differences are limited to the males being slightly more pigmented than the females.

Remarks on Osteology and Comparison to Other Pereleotrines

With few exceptions, the osteological characters of *Aioliops* match those described by Hoese (1984) for the subfamily Ptereleotrinae: separate dorsal fins, articular process of the premaxilla fused with the ascending process and a single pterygiophore preceding the first hemal spine. Distinguishing osteological features of *Aioliops* are: no lacrimal, cartilaginous rostral, sphenotic separated from supraoccipital by cartilage, frontal not extending between sphenotic and supraoccipital, prominent dorsolateral process near posterior end of anguloarticular and, with the exception of *A. brachypterus,* open neural arches with slightly elevated basal portions and no lateral foramen on the caudal vertebrae.

In external morphology, species of *Aioliops* are distinguishable from other genera in having: 2 or 3 preopercular pores; one interorbital head pore which is paired laterally; oblique mouth; large, ctenoid scales or no scales; anterior nostril a short tube or a simple pore; pelvic fins with 3–4 segmented rays; second dorsal fin I, 9–10; anal fin I, 9–11; and gill opening extending to below or behind the posterior margin of the preoperculum.

Allied genera are *Parioglossus* Regan (revised by Rennis & Hoese, 1985), *Nemateleotris* Fowler (revised by Randall & Allen, 1973), *Ptereleotris* Gill (revised by Randall & Hoese, 1985) and *Oxymetopon* Bleeker (revised by Klausewitz & Conde, 1981). Comparisons of certain characters are shown in Tables 1 and 2.

When first discovered by D.F.H., it was believed that *Aioliops* was most closely related to *Parioglossus.* This was based on the similarity in head pore pattern, small size and low number of dorsal and anal rays in the two genera. Both genera also have laterally paired interorbital pores, but, since the posterior interorbital pore is often paired in juveniles of gobioid fishes, it was considered possible that this pattern was simply related to the small size of the species in the two genera. Examination of external features and osteological features, however, suggested that the two genera were not as closely related as initially thought. Because the relationships of the ptereleotrines are not known, character state polarities discussed below were hypothesized, where possible, from eleotridid fishes.

Most species of eleotridids have ctenoid scales, but species with cycloid scales do occur. Similarly, preopercular pores are often absent, but when present, there are usually 4–6 pores. The anterior interorbital head canals are separate in eleotridids. Although ontogenetically, the interorbital pores begin development as paired pores, in some genera the posterior interorbital pore is median and connected by tubes to both canals. All eleotridid genera have 5 segmented pelvic rays, have some ossification of the

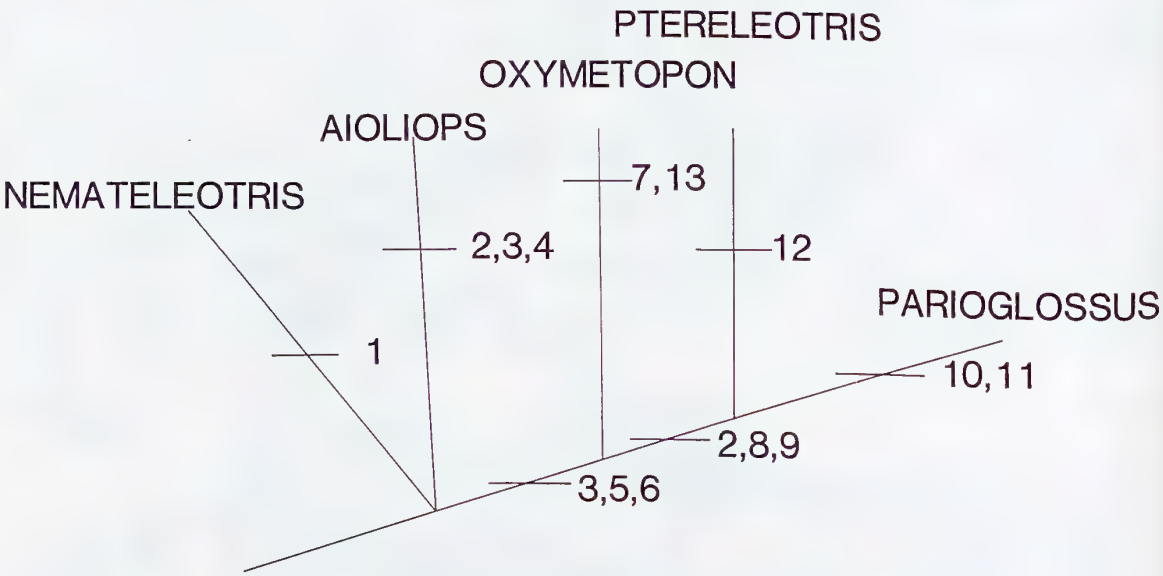

Fig. 17. Tentative phylogeny of the Ptereleotrinae based on some osteological and other morphological characters (see 'Remarks on osteology and comparison to other ptereleotrines' section for discussion of character state polarities). The following characters are interpreted to be advanced character state polarities: **1,** elongate dorsal fin spines; **2,** cartilaginous scapula; **3,** reduced number of pelvic-fin rays; **4,** lacrimal absent; **5,** vertical palatopterygoid strut; **6,** articular process of premaxilla subequal to ascending process; **7,** body and head compressed; **8,** cycloid or no scales; **9,** reduced preopercular pore number; **10,** terminal canal pore absent, **11,** prominent anterior zygapophyses on all precaudal and most caudal vertebrae; **12,** pterygiophore formula of 3(32010); **13,** bony frontal.

scapula, have a mouth that is only slightly oblique with a very oblique palatopterygoid strut, have separate ascending and articular processes of the premaxillae, have a well developed lacrimal, and have zygapophyses that are poorly developed. When pores are present, the lateral canal is typically well developed in primitive eleotridids.

Species of *Nemateleotris* appear to be the most primitive of the ptereleotrines in having ctenoid scales over most of the body, 3 preopercular pores, 5 segmented pelvic rays and a dorsolateral process on the anguloarticular for the attachment of a tendon of the adductor mandibulae. The process is present or absent in eleotridids, but is presumed primitive here. Species of *Ptereleotris* and *Parioglossus* are clearly specialized in several features in relation to those of *Nemateleotris*. Members of both genera have a highly oblique, protrusible mouth, with the palatopterygoid strut being almost vertical (5)(number refers to Fig. 17), numerous small, cycloid scales (8), 4 segmented pelvic rays (3), a poorly ossified or cartilaginous scapula (2), 0 or 2 preopercular pores (9) and very elongate ascending and articular processes of the premaxilla (6)(the two processes are connected to each other near the tip in ptereleotrines). Species of both genera also lack or have a rudimentary dorsolateral process on the anguloarticular for the attachment of a tendon of the adductor maxillae. *Ptereleotris* species are specialized and unique in exhibiting the pterygiophore formula of 3(32010) (12), while *Parioglossus* species are specialized in lacking the terminal lateral canal pore above the preoperculum (10) and prominent development of anterior zygapophyses (11). Consequently, it is suggested here that *Nemateleotris* is the sister group to *Ptereleotris* and *Parioglossus*. Species of *Nemateleotris* are presumably specialized in the filamentous anterior spines of the first dorsal fin (1). Filamentous spines occur in the other genera, but these are usually middle or posterior spines and are not as strongly developed as those of *Nemateleotris*. Species of *Oxymetopon* share with *Ptereleotris* and *Parioglossus* species the highly protrusible mouth and almost vertical palatopterygoid strut (5), but display the more primitive features of ossified scapula, ctenoid scales on the body, scales on the head and 3 preopercular pores. *Oxymetopon* species are specialized in the strongly compressed head and body (7), with a prominent bony, median frontal (13)and large supraoccipital crest. In the single cleared and stained specimen examined, only the dorsal section of the rostral cartilage stained with alcian blue, and if found in all species of *Oxymetopon,* this feature may also prove to be a specialization, since in other gobioids with an unossified rostral the rostral stains evenly with alcian blue. Therefore, it appears most likely that members of the genus *Oxymetopon* form the primitive sister group to *Ptereleotris* and *Parioglossus* species, with *Nemateleotris* forming the sister group to these genera.

The relationships of *Aioliops* are not as clear. The members of the genus appear primitive in having moderately sized, ctenoid scales (although one species has no scales), 3 preopercular pores in some species, slightly protrusible mouth and oblique palatopterygoid strut. Species are specialized in the absence of a lacrimal (4). The process on the anguloarticular for the tendon attachment of the adductor maxillae is very large, and this may represent the primitive condition or a specialization in relation to species of *Nemateleotris*. The only specializations in common with *Ptereleotris* and *Parioglossus* are the reduction in ossification of the scapula (2) and reduced number of pelvic rays (3). Reduction in ossification of the scapula is common in small-sized gobioids, and reduction in pelvic-ray numbers also occurs among various other gobioid fishes. As one species of *Aioliops* has a further reduced number of pelvic-fin rays compared to other species, it is difficult to determine whether pelvic-fin ray reduction occurred independently from *Nemateleotris* with species of *Nemateleotris* and *Aioliops* evolving from the same parental taxa, and the character being homoplasous for the other genera, or whether *Nemateleotris* forms the primitive sister group to all the other genera. *Aioliops* also presents problems as the small size of the species may be one reason why certain characters are not present or are reduced. Because its relationships are unclear and several character states are unresolved, it remains ambiguous as to whether *Nemateleotris* and *Aioliops* collectively form a primitive sister group to *Oxymetopon, Parioglossus* and *Ptereleotris* (Fig. 17), or whether *Aioliops* forms a sister group to other ptereleotrines or to *Parioglossus* and *Ptereleotris.*

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References

Birdsong, R.S., 1975. The osteology of *Microgobius signatus* Poey (Pisces: Gobiidae), with comments on other gobiid fishes. Bulletin Florida State Museum, Biological Sciences 19: 135–186.

Dawson, C.E., 1974. A review of the Microdesmidae (Pisces: Gobioidea) 1. *Cerdale* and *Clarkichthys* with descriptions of three new species. Copeia 1974(2): 409–448.

Gosline, W.A., 1955. The osteology and relationships of certain gobioid fishes, with particular reference to the genera *Kraemeria* and *Microdesmus*. Pacific Science 9: 158–170.

Hoese, D.F., 1984. Gobioidei: Relationships. **In** "Ontogeny and Systematics of Fishes" (Moser, H.G., W.J. Richards, D.M. Cohen, M.P. Fahay, A.W. Kendall, Jr., & S.L. Richardson, eds): 588–591. American Society of Ichthyologists and Herpetologists, Special Publication Number 1: 760 pp.

Hubbs, C.L. & K.F. Lagler, 1974. Fishes of the Great Lakes region. University of Michigan Press, Ann Arbor, U.S.A., pp. 135.

Klausewitz, W. & B. Conde, 1981. *Oxymetopon cyanoctenosus,* n. sp., un nouvel Eleotride des Philippines, avec une etude comparee du genre (Pisces, Perciformes, Gobioidei, Eleotridae). Revue Francaise d'Aquariology 8(3): 67–76.

Leviton, A.E., R.H. Gibbs Jr., E. Heal, & C.E. Dawson, 1985. Standards in Herpetology and Ichthyology: Part I. Standard symbolic codes for institutional resource collections in Herpetology and Ichthyology. Copeia 1985(3): 802–832.

Miller, P.J., 1973. The osteology and adaptive features of *Rhyacichthys aspro* (Teleostei: Gobioidei) and the classification of gobioid fishes. Journal of Zoology, London 171: 397–434.

Randall, J.E. & G.R. Allen, 1973. A revision of the gobiid fish genus *Nemateleotris,* with descriptions of two new species. Quarterly Journal of the Taiwan Museum 26(3,4): 347–367.

Randall, J.E. & D.F. Hoese, 1985. Revision of the dartfishes, Genus *Ptereleotris* (Perciformes: Gobioidei). Indo-Pacific Fishes 7: 1–36.

Regan, C.T., 1911. The osteology and classification of the gobioid fishes. Annals and Magazine of Natural History, Series 8, 8(48): 729–733.

Rennis, D.S. & D.F. Hoese, 1985. A review of the genus *Parioglossus,* with descriptions of six new species (Pisces: Gobioidei). Records of the Australian Museum 36: 169–201.

Springer, V.G., 1983. *Tyson belos,* new genus and species of western Pacific fish (Gobiidae, Xenisthminae), with discussions of gobioid osteology and classification. Smithsonian Contributions to Zoology 390: 1–40.

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Australian *Pleopodias* Richardson, 1910, and *Anilocra* Leach, 1818 (Isopoda: Cymothoidae), crustacean parasites of marine fishes ..... NEIL L. BRUCE 85

Australian *Pleopodias* Richardson, 1910, and *Anilocra* Leach, 1818 (Isopoda: Cymothoidae), Crustacean Parasites of Marine Fishes

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ABSTRACT. The genus *Pleopodias* is recorded from Australia for the first time. The genus is rediagnosed, and figures given for *Pleopodias* sp. and *P. elongatus* Richardson. Twelve Australian species of *Anilocra* are described and figured: *A. alloceracea* Koelbel, *A. caudata* Bovallius, *A. dimidiata* Bleeker, *A. leptosoma* Bleeker, *A. longicauda* Schiödte & Meinert, *A. ankistra* n. sp., *A. apogonae* n. sp., *A. koolanae* n. sp., *A. morsicata* n. sp., *A. nemipteri* n. sp., *A. pomacentri* n. sp., and *A. soelae* n. sp. Additional figures and descriptive notes are given for *A. cavicauda* Richardson, that species being revalidated. *Anilocra carpentariensis* Avdeev is synonymised with *A. dimidiata*. Keys are provided for the Australian genera of the *Anilocra* group, and the Australian species of *Anilocra*.

BRUCE, N.L., 1987. Australian *Plepodias* Richardson, 1910, and *Anilocra* Leach, 1818 (Isopoda: Cymothoidae), crustacean parasites of marine fishes. Records of the Australian Museum 39(2): 85–130.

Recent studies of the Australian Cymothoidae were limited to the work of Hale (1926, 1940) and Avdeev (1975a,b,c, 1977, 1978, 1979a,b,c), the latter publishing on material collected around, but beyond Australian territorial waters. More recently, Bruce (1986) recorded 9 species of *Mothocya* from Australian waters. Prior to the work of Hale (1926) the only information available on Australian cymothoids was that to be found in the monographs of Schiödte & Meinert (1881, 1883, 1884). Other early works of relevance to the Australian cymothoid fauna are those dealing with the Indo-Pacific (Bleeker, 1857; Bovallius, 1887; Haller, 1880; Koelbel, 1878; Miers, 1880; Nierstrasz, 1915, 1918; Richardson, 1910). Some of these early publications (Haller, 1880; Miers, 1880) are of particular importance as they were not seen by Schiödte & Meinert, and the names proposed may have priority over those proposed by Schiödte & Meinert.

Up to and including Avdeev's publications, 45 species of Cymothoidae in nine genera had been recorded from waters around Australia. Of these, *Nerocila* and *Anilocra* were the only genera of the epidermal attaching lineage of Brusca (1981). Two species of *Anilocra* have been recorded from Australia: *Anilocra cavicauda,* a misidentification of Hale (1926), and *A. carpentariensis* which is here synonymised with *A. dimidiata*. *Renocila* and *Nerocila* are well represented in Australian waters, and accounts of these two genera will be given in later publications.

Little is known about endemicity or distributional patterns of genera and species of Indo-Pacific Cymothoidae. Avdeev (1985) discussed the distribution of marine cymothoids but, as this present work and other recent publications (Williams & Williams, 1980, 1981; Bruce, 1986) have demonstrated, species richness within the Cymothoidae is far greater than previously suspected.

Methods

When host specimens have been available, identifications have been confirmed by the staff of the Australian Museum Fish Section. Host identifications of specimens not retained, or non-expert identifications are marked by an asterisk. Host identifications without the specimen have been given in the original combination in the 'Material examined' section, and the most recent combination in the 'Hosts' section.

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All pereopods within a species description are drawn to the same scale, as are all pleopods. All measurements are of length measured from the anterior margin of the cephalon to the apex of the pleotelson, and are in millimetres.

Material placed in the 'Additional material' section is that which has been identified as belonging to the species, but has not been studied in detail.

Abbreviations

AM	Australian Museum, Sydney, NSW, Australia
CSIRO	Commonwealth, Industrial and Scientific Research Organisation, Australia
MNHN	Muséum National d'Histoire Naturelle, Paris, France
NMV	Museum of Victoria, Melbourne, Australia
NRS	Naturhistoriska Riksmuseet, Stockholm, Sweden
NT	Northern Territory, Australia
NTM	Northern Territory Museum, Darwin, Australia
Qld	Queensland, Australia
QFS	Queensland Fisheries Service
QM	Queensland Museum, Brisbane
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands
SAM	South Australian Museum, Adelaide
USNM	Smithsonian Institution, Washington, D.C., U.S.A.
WA	Western Australia
WAM	Western Australian Musuem, Perth
ZMC	Zoologisk Museum, Copenhagen.

Taxonomy

Brusca (1981) recognised three lineages within the Cymothoidae. Those genera related to *Anilocra* and *Nerocila* which attach to the hosts' outer body surface form the externally attaching lineage. The other two lineages are the buccal-gill attaching lineage and those genera that burrow into the hosts flesh. Brusca (1981) considered the latter to be polyphletic. Although the *Anilocra* group of genera can be easily separated on ecological criteria, they can be distinguished from all other cymothoids by morphological characters as well. These characters are: body bilaterally symmetrical; cephalon weakly immersed in pereonite 1; body and appendages usually with abundant chromatophores; brood pouch with oostegites of pereonite 6 dominant (those of pereonites 2, 3, 4 and 6 subequal in other cymothoids) and with posterior pocket arising from sternite 7 (absent in other cymothoids); pereopods without laminar extensions to basis, without bulbous articles; pereopod 7 frequently with spines.

Three inadequately described genera of the epidermal-attaching lineage have been recorded from the Indo-Pacific. Brief remarks for these genera are given here to aid in their identification should they be found in Australia. They are not included in the generic key as none of these genera has been described in detail.

Amblycephalon Pillai, 1954: described in more detail by Pillai (1963). Monotypic; differing from *Anilocra* and *Pleopodias* by lacking reflexed rostrum and having posterior angles of coxae of pereonites 4–7 produced to posterior of their segment; *Nerocila* differs in having ventrolateral extensions on pleonites 1 and 2; *Renocila* differs in having posterolateral margins of pereonites 5–7 produced. Antennule, antenna and mandibles same as those of *Nerocila*. Recorded only from India (Pillai, 1963).

Plotor Schiödte & Meinert, 1881: monotypic; differing from *Nerocila* by lacking ventrolateral extensions on pleonites 1 and 2. Known only from Indian Ocean, 4°30′S, 137°E (Schiödte & Meinert, 1881).

Rosca Schiödte & Meinert, 1881. Two species have been placed in this genus: *R. limbata* Schiödte & Meinert, 1881, from Amboina, and *R. rogans* Stebbing, 1924. The type of the latter is an intermoult juvenile of *Nerocila orbignyi* (see Barnard, 1950). *Rosca limbata* differs from *Nerocila* by the cephalon posterior margin not being trilobed.

Key to Australian Genera of the *Anilocra* Group

1. Cephalon posterior margin trisinuate; pleonites 1 and 2 with ventrolateral margins produced; body dorsoventrally flattened; coxae 5–7 as long or longer than respective pereonite. ..... *Nerocila*

——Cephalon posterior margin straight or smoothly curved; pleonites 1 and 2 with ventrolateral margins not produced; body dorsal surface strongly vaulted; coxae 5–7 manifestly shorter than respective pereonite. 2

2. Cephalon without rostrum, or rostrum not projecting between antennule bases; antennule as long as, or longer than antenna; posterolateral margins of pereonites 5–7 produced; coxae 5–7 posteriorly acute. ..... *Renocila*

——Rostrum folded back, lying between antennule bases; antennule shorter than antenna; posterolateral margins of pereonites 5–7 not produced; coxae posteriorly rounded. 3

3. Mandible palp article 3 shorter than article 2; maxilla with 2 short spines each on medial and lateral lobe, medial lobe partially fused to lateral; antennule articles 4–8 short (e.g. Fig. 5d, 10d); posterior of pleon about 0.7 width of pereon. ..... *Anilocra*

——Mandible palp article 3 longer than article 2; maxilla with 2 large nodular spines each an medial and lateral lobe, medial lobe distinct; antennule articles 4–8 elongate (Fig. 1i); posterior of pleon about 0.35 width of pereon. ..... *Pleopodias*

Pleopodias Richardson

Pleopodias Richardson, 1910: 25.—Barnard, 1936: 166.

Diagnosis of female. Cephalon posterior margin not trilobed; rostrum anterior margin folded back, concealing proximal article of antennule. Posterolateral margins of pereonites not produced. Coxae 2 and 3 as long as respective pereonite, coxae 4–7 narrow, always shorter than respective pereonite. Pleon much narrower than pereon, width of pleonites decreasing markedly towards posterior.

Antennule bases close set, both antennule and antenna dorsoventrally flattened, antennule articles 2 and 3 expanded; articles 4–8 elongate. Mandible palp article 3 slender, longer than article 2. Maxilla medial lobe distinct; 2 nodulose spines each on medial and lateral lobe respectively. Pleopods conspicuous in dorsal view, peduncles without accessory lobes; pleopods 1–4 with lamellar rami, endopod of pleopod 5 with 3 simple folds, exopod lamellar.

Additional characters. Eyes present, facets distinct. Pereon dorsum strongly vaulted, widest at pereonites 5 and 6; pereonite 2 shortest, 6 longest. Pleonites 1 and 2 with lateral and ventrolateral margins not produced. Pleotelson narrow, lateral margins bent up.

Maxillule with 3 terminal spines. Pereopods 1–4 short, progressively increasing in length; pereopods 5 and 6 longer than 1–4; pereopod 7 markedly longer than 6, and about 2.3 times longer than pereopod 1. Brood pouch formed by 2 large oostegites arising from pereonite 5, smaller oostegites on pereonites 1, 2, 3 and 4, and posterior pocket. Endopod of pleopods 1 and without, and 3–5 with proximomedial lobe; endopods of pleopods 1–5 progressively decreasing in length. Uropod peduncle and rami elongate.

Type species. *Pleopodias elongatus* Richardson, 1910, by monotypy.

Remarks. The genus *Pleopodias* has received little attention since it was established. Richardson (1911) described a second species from the tropical eastern Atlantic, *P. vigilans,* but gave no figures, nor further discussion on the genus. Barnard (1936) questioned the significance of characters used by Richardson to define the genus, correctly pointing out that several species of *Anilocra* have pleopods prominent in dorsal view and have antennule articles 2 and 3 expanded.

Examination of the type specimen of *P. elongatus* and the specimen from Western Australia revealed several characters by which the two genera are separated. In *Pleopodias* these are: pleon narrowing strongly towards posterior, and much narrower than pereon (not posteriorly narrower in *Anilocra);* antennule articles 4–8 elongate (short in *Anilocra);* maxilla medial lobe distinct (partially fused in *Anilocra);* prominent and nodulose spines on the maxilla (small, simple spines in *Anilocra);* mandible palp article 3 slender, longer than article 2 (robust, shorter than article 2 in *Anilocra);* and pereopod 7 far more spinose than that of *Anilocra.*

Pleopodias sp.

Figs 1, 2

Pleopodias elongatus.—Barnard, 1936: 167, fig. 7f,g (not *P. elongatus* Richardson, 1910).

Material examined. Female (ovig 14.5, crushed in tube), 232 k north of Port Hedland, WA, 18°10′S, 118°18′E, 10 Oct 1982, depth 298–300 m, coll L. Marsh & S. Slack-Smith on FRV *Soela* (WAM 607-80).

Description. Rostrum strongly produced, lateral margins concave; eyes large, about 0.6 width of cephalon. Pleonite 5 about 0.4 width of pereonite 7. Pleotelson about 2.7 times as long as wide.

Antennule with 8 articles, 2 and 3 wide, 5–8 slender; extends to posterior of pereonite 1. Antenna with 13 articles, articles 1–3 short, 4–7 long, 8–13 becoming progressively shorter.

Mandible palp article 3, 3 times as long as wide. Maxilla medial lobe with 1 smooth spine and 1 nodulose spine, lateral lobe with both spines nodulose. Maxilliped article 3 with 3 spines.

Pereopods 1–3 with dactylus robust, without nodules. Pereopod 6 merus nearly twice as long as carpus; propodus posterior margin with scattered small spines. Pereopod 7 with medial surfaces of carpus and propodus densely covered with small spines.

Pleopod 1 peduncle slightly more than 4 times as long as wide, peduncles of pleopods 2–5 becoming progressively narrower towards posterior. Pleopod 1 rami distal margins rounded, pleopods 2–5 with rami becoming progressively narrower. Pleopod 2 with appendix masculina. Uropod peduncle about 4 times as long as wide; rami subequal in length, extending clearly beyond posterior of pleotelson.

Colour. Dark reddish brown in alcohol.

Size. 14.5–15.5 mm (Barnard, 1936).

Remarks. The specimen described here, while

undoudtedly distict from *P. elongatus* cannot be described as a new species owing to its crushed condition. The Australian specimen differs from *P. elongatus* in being smaller in size, having a far narrower pleotelson, shorter rostrum, larger eyes, narrower pleopod peduncles, and retaining the appendix masculina. Barnard's (1936) figures agree well with Western Australian material, and that record is here considered conspecific with the Australian specimen.

Hosts. Not known.

Distribution. Andaman Islands, north-eastern Indian Ocean (Barnard, 1936) and north-western Australia; to depths of 300 metres.

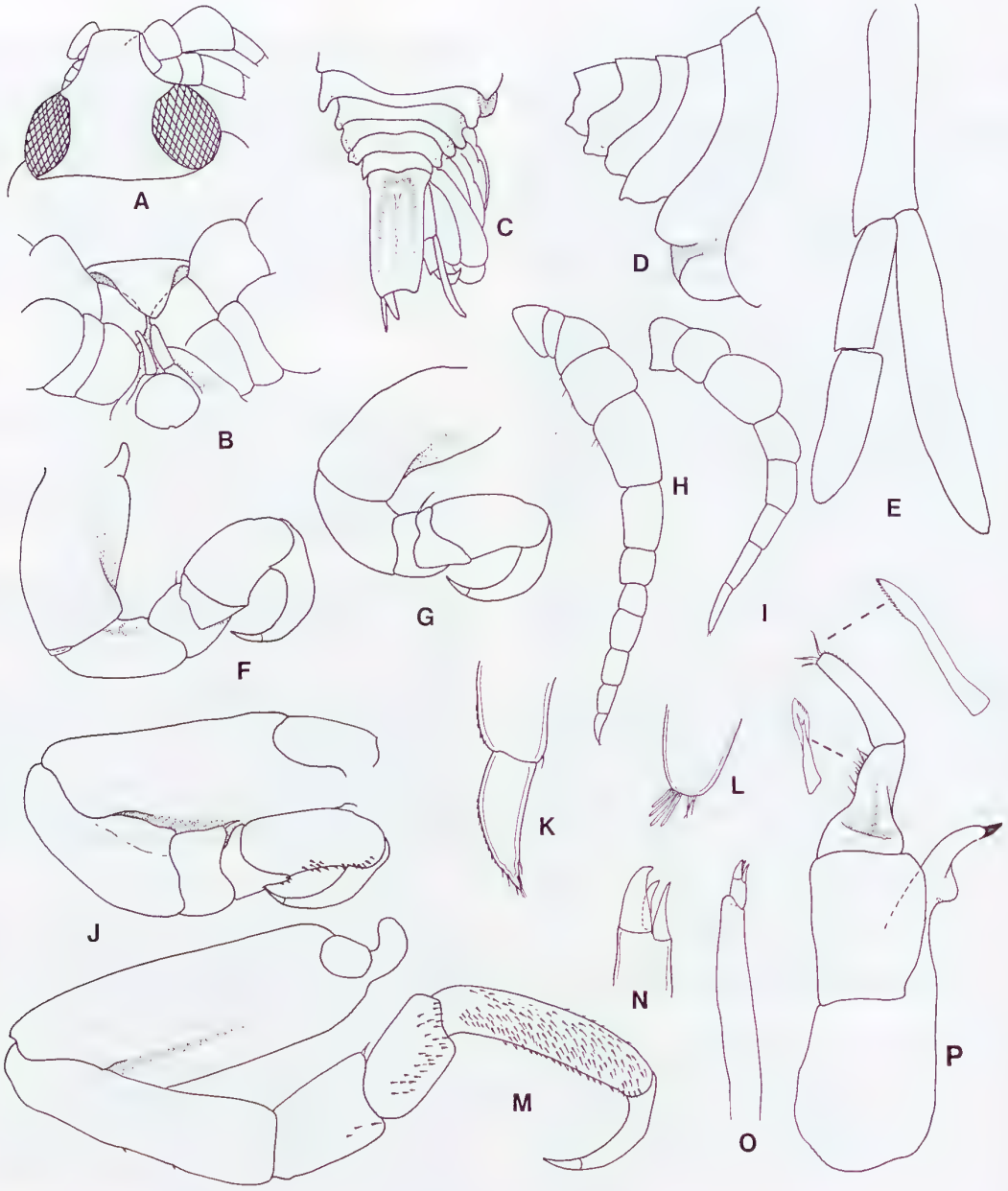

Fig. 1. *Pleopodias* sp. (WAM 607-80). **A**, cephalon; **B**, frons; **C**, pleon and pleotelson, dorsal view; **D**, pleon, lateral view; **E**, uropod; **F**, pereopod 1; **G**, pereopod 2; **H**, antenna; **I**, antennule; **J**, pereopod 6; **K**, antenna, terminal article; **L**, antennule, apex of terminal article; **M**, pereopod 7; **N**, maxillule apex; **O**, maxillule (apex creased); **P**, mandible.

Pleopodias elongatus Richardson

Fig. 3

Pleopodias elongatus Richardson, 1910: 26, fig. 25.—Nierstrasz, 1931: 133.

Material examined. HOLOTYPE: female (ovig 20.0), off Motocot Point, Philippine Islands, 8 June 1908, 170 fathoms (= 306 m), coll U.S. Bureau of Fisheries *Albatross* Philippine Expedition 1907–08 (USNM 40917).

Descriptive notes. Body about 2.5 times as long as wide; lateral margins sub-parallel in dorsal view. Eyes about 0.5 width of cephalon; rostrum strongly produced, lateral margins weakly concave. Pleotelson about 1.6 times as long as wide, lateral margins weakly convex, posterior margin rounded.

Antennule bases not contiguous. Mandible palp article 2 with numerous setae along lateral margin. Maxilla medial lobe with 1 large conical spine and 1 small spine. Pereopods similar to those of *Pleopodias* sp. Pleopod 2 without appendix masculina.

Remarks. As discussed under the remarks for *Pleopodias* sp., *P. elongatus* is clearly distinct from the Indian Ocean species. Additional figures are given here to facilitate identification of the species.

Hosts. Not known.

Distribution. Philippine Islands.

Anilocra Leach

Anilocra Leach, 1818: 348, 350.—Desmarest, 1825: 306; Edwards, 1840: 255; Dana, 1853: 747; Schiödte & Meinert, 1881: 100; Gerstaecker, 1882: 231; Richardson, 1905: 25; Hale, 1926: 210; Schultz, 1969: 153; Kensley, 1978: 78; Kussakin, 1979: 281; Brusca, 1981: 140; Brusca & Iverson, 1985: 45.

Canolira Leach, 1818: 350.

Epichthyes Herklots, 1870: 122.

Diagnosis of female. Cephalon posterior margin weakly or not trilobed; rostrum anterior portion folded down and back, not concealing antennule basal articles. Coxae 2 and 3 as long as respective pereonite; coxae 4–7 narrow, much shorter than respective pereonite. Posterolateral margins of pereonites not produced. Pleonites all visible, pleon lateral margins sub-parallel or narrowing slightly towards posterior.

Mandible palp articles robust, article 3 setose, shorter than article 2. Pereopods 1–4 short, 5–6 longer; pereopod 7 markedly longer than 6, 1.7–2.9 times longer

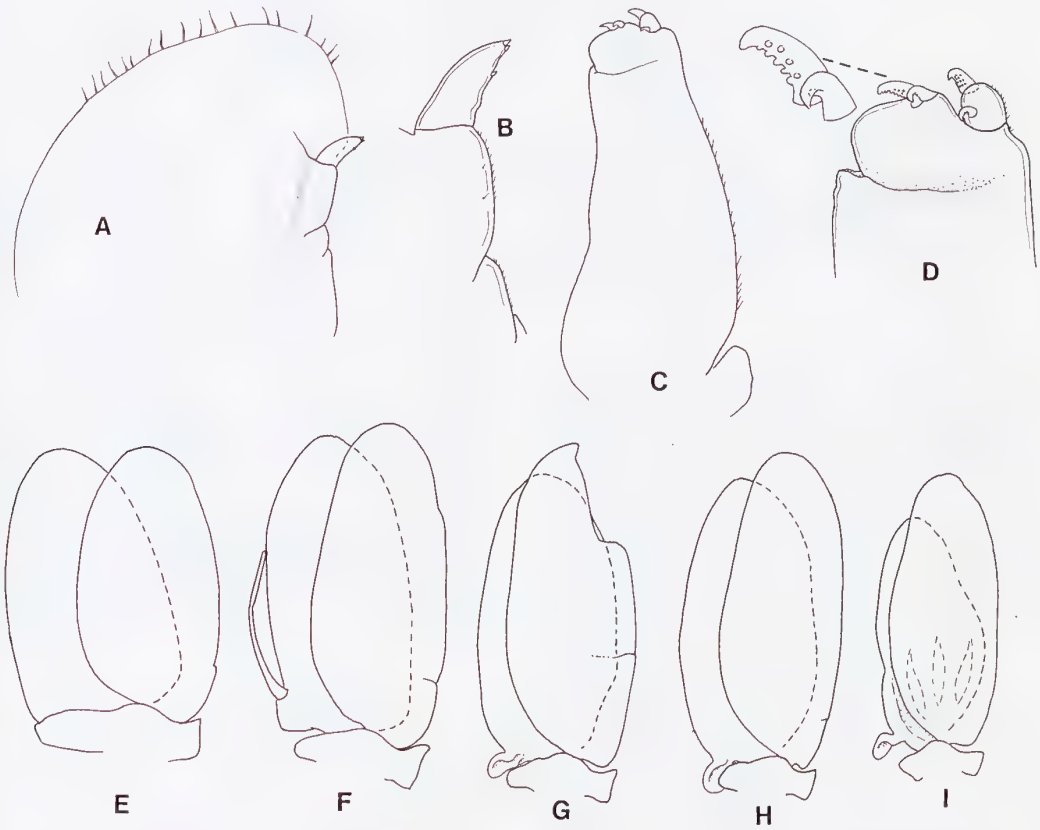

Fig. 2. *Pleopodias* sp. (WAM 607-80). **A**, maxilliped; **B**, maxilliped detail; **C**, maxilla; **D**, maxilla apex; **E–I**, pleopods 1–5 respectively.

than pereopod 1. Pleopods visible in dorsal view; peduncles without accessory lobes. Endopods of pleopods 1 without, and 3–5 with proximomedial lobe.

Additional characters. Pereon dorsum strongly vaulted, widest at pereonites 5 and 6; pereonite 2 shortest, 6 longest, pereonite 7 usually about 0.6 as long (0.45–0.81) as pereonite 6. Pleotelson longer than wide. Pleonite lateral and ventrolateral margins not produced.

Antennule usually with 8 articles, bases not contiguous; articles 1–3 more robust than remainder; articles 4–8 short. Antenna longer than antennule. Maxillule with 3 or 4 terminal spines. Maxilla medial lobe partially fused to lateral lobe, each lobe with 2 small stout spines. Maxilliped article 3 with 3 or 4 short curved spines. Brood pouch formed by 2 large oostegites arising from pereonite 5, smaller oostegites from pereonites 1, 2, 3 and 4, and posterior pocket. Pleopods 1 and 2 each with lamellar rami, pleopods 3 and 4 usually with small folded lobes on posterior surface of endopod; pleopod 5 endopod with prominent folded lobes; endopod of pleopod 5 subtruncate. Endopods decreasing in length from pleopod 1 to pleopod 5. Uropod peduncle and rami elongate.

Male. Smaller, narrower than female; eyes proportionally larger. Pleon and pleotelson characters may not be developed. Appendages generally similar to

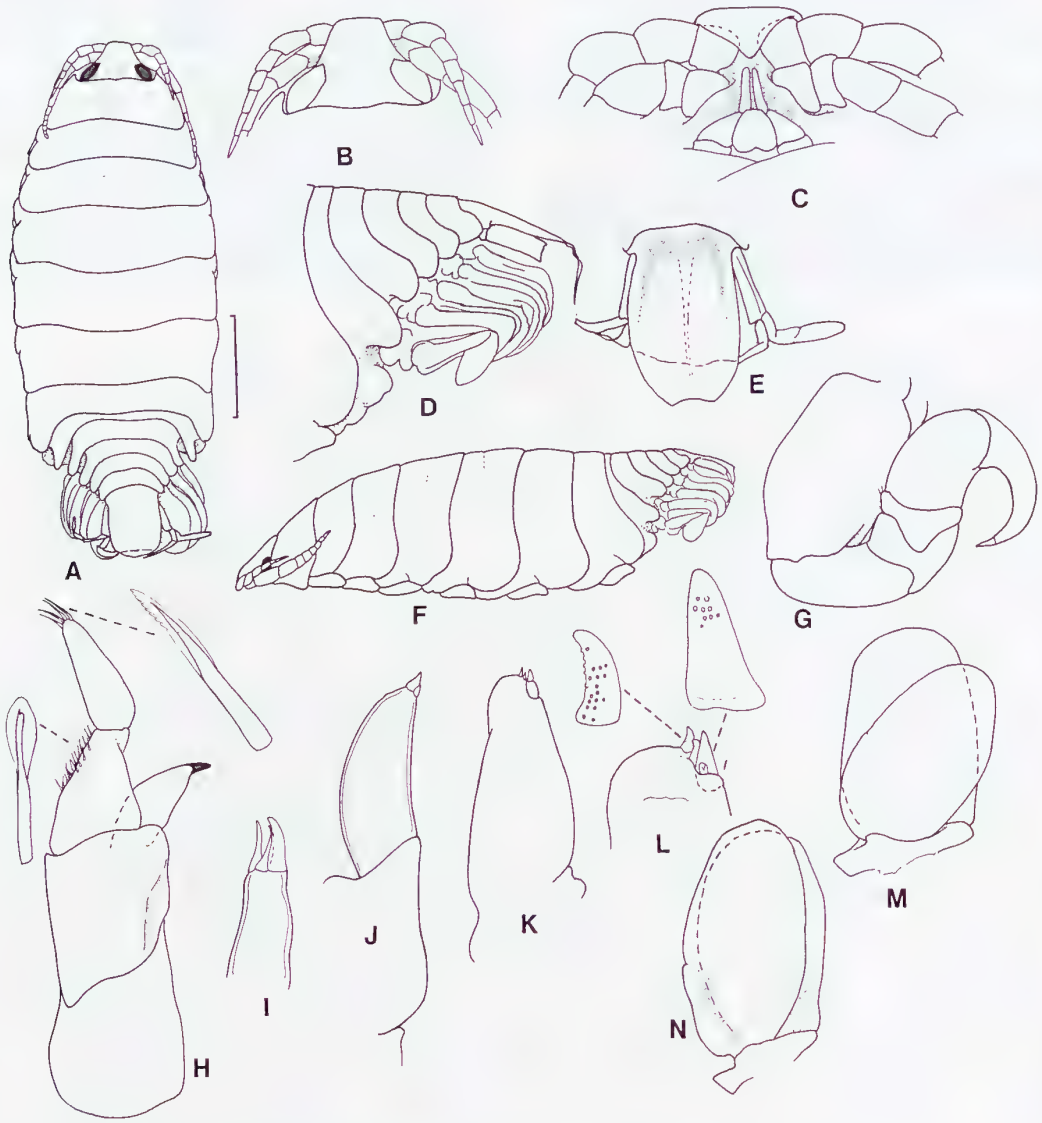

Fig. 3. *Pleopodias elongatus,* holotype (USNM 40917). **A,** dorsal view; **B,** cephalon, dorsal view; **C,** frons; **D,** pleon, lateral view; **E,** pleotelson (straightened); **F,** lateral view; **G,** pereopod 1, in situ; **H,** mandible; **I,** maxillule apex; **J,** maxilliped articles 2, 3; **K,** maxilla; **L,** maxilla, apex and detail of spines; **M,** pleopod 1; **N,** pleopod 2. Scale line represents 4.0 mm.

female except maxilliped article 3 with larger terminal spines, pereopod with dactylus nodules not fully developed. Pleopod 2 with appendix masculina, folding on endopods of pleopods 3–5 less well developed. Penial process not present (in species examined here).

Type species. Leach (1818), in establishing the genus, recorded three species. Kussakin (1979) designated *Anilocra cuvieri,* the first described in Leach's text, as the type species. *Anilocra cuvieri* is a synonym of *Anilocra physodes* (Linnaeus, 1758) (see Trilles, 1975, for synonymy), and the type specimen of *A. physodes* is held at the British Museum (Natural History) (1758: 636).

Remarks. The genus *Anilocra,* currently with about 37 species, is primarily tropical in distribution. Only three eastern Atlantic species extend beyond the tropics (Trilles, 1975). *Anilocra frontalis* occurs off the Dutch coast at latitude 53°33′N (Holthuis, 1978). In Australia, the most southerly records of *Anilocra* are of *A. leptosoma* and *A. apogonae,* both of which occur in Moreton Bay, southern Queensland (ca. 27°S). The distribution of Australian *Pleopodias* and *Anilocra* is given in Figure 33.

There are two areas of high diversity, the West Indies with nine species, and the Australian-Malaysian region with 18 species. The eastern Atlantic has three species, while the Indian and Pacific Oceans (excluding Australia) have 14 species, seven of which are from the Malaysian-Indonesian area.

Characters which separate *Anilocra* from related genera are to be found in the key. *Anilocra* is distinguished from *Pleopodias* by the obviously wider pleon and pleotelson, shorter antennule articles, shorter mandible palp article 3, and the character differences listed under the remarks for *Pleopodias.*

Types of four Indo-Pacific species were either not located (*A. australis* Schiödte & Meinert, 1881, and *A. alloceraea* Koelbel, 1878), or not made available for study (*A. acuminata* Haller, 1880, and *A. tropica* Avdeev, 1977). The status of these species, with the exception of *A. alloceraea,* is uncertain, and they cannot be separated from others of the genus with any confidence. *Anilocra australis* is characterised by a very short uropod endopod. *Anilocra tropica* is apparently characterised by a very wide pleon, short subequal uropod rami, and pereopod 7 with very large spines which occur on the merus, propodus, and uniquely, on the dactylus (Avdeev, 1977, fig 2). Little can be said of *Anilocra acuminata,* but that it could be one of many Indo-Pacific species.

Characters of Taxonomic Utility

Cephalon: rostrum: width, length; eye size. Pereon: relative width. Pleon: relative length of pleonite 1; relative width; details of posterolateral angles of pleonites 4 and 5; detail of lateral margins of pleonites 1–4. Pleotelson: shape; lateral margins flat or upturned.

Antennule and antenna: relative lengths of both, number of articles present in antenna; antennule article 3 produced or not. Mouthparts: mandible palp; details of maxilla and maxilliped may often be supportive characters. Pereopods: shape of, and presence and distribution of nodules on dactylus of pereopods 1–4; density of spines on pereopod 7; relative length of pereopod 7 compared to pereopod 1. Pleopods: shape and width; degree of folding on pleopods 3–5; presence or absence of appendix masculina. Uropods: shape; relative lengths of rami; extension beyond pleotelson or not.

Host Preferences

Recent work by Williams & Williams (1981) demonstrated that *Anilocra* species have a higher degree of host specificity than previously suspected. Prior to their revision of the Caribbean *Anilocra,* most specimens were attributed to *Anilocra laticauda* which had been recorded from hosts of 11 fish families (Trilles & Vala, 1975). Williams & Williams (1981) found *A. laticauda* to be a *nomen dubium,* and recorded nine species of *Anilocra* from the West Indies. Of these, five were recorded from a single host species, three were from two to four species within a genus, and one from nine host species from three genera of Serranidae. This suggests a strong correlation between isopod and host family, but varying degrees of specificity at low levels of host classification.

Half of the Australian species recorded here lack host data. The remainder suggest a pattern similar to that of West Indian *Anilocra:* close affinity to a host family, lower specificity to genus and species. *Anilocra apogonae* is recorded from five host species in two genera of Apogonidae. *Anilocra nemipteri* from seven species in three genera of Nemipteridae, and also one species of Pomacentridae. *Anilocra pomacentri* is recorded from ten species in three genera of Pomacentridae.

Host preference on the Great Barrier Reef appears to be strongly localised. At Lizard Island, *Anilocra pomacentri* utilises *Pomacentrus melanochir* and *P. pavo,* while on Heron Island and adjacent Wistari Reef it has been recorded only from *Chromis nitidus.* In the Palm Group, these three hosts are present, but *A. pomacentri* occurs commonly on *Pomacentrus melanopterus, Pomacentrus lepidogenys* and *Pomacentrus moluccensis. Anilocra nemipteri* occurs commonly on *Scolopsis bilineatus* at Lizard Island. It is not found on that host in the Palm Group but on *Scolopsis monogramma* and *Pentapodus setosus.* Table 1 summarises host data for Australian species of *Anilocra.*

In areas of high host species diversity (West Indies, central Indo-Pacific) *Anilocra* species are found on a limited number of host species, usually within one or two genera. In areas of lower diversity, the isopod can utilise a greater number of hosts, perhaps through reduced competitive pressure. An example is the north-eastern Atlantic and Mediterranean species *Anilocra physodes* which has been recorded from 25 genera in

13 families (Trilles, 1975a). *Anilocra monoma* from Kuwait was recorded from 4 host species in 4 families (Bowman & Tareen, 1983), a pattern inconsistent with that of other tropical *Anilocra*. *Anilocra monoma* has no recorded sympatric congeners, and again, this may allow it to utilise a wider array of hosts.

Table 1. Australian species of *Anilocra* with their recorded hosts (* = unconfirmed record; † = isopod sight record; GBR = Great Barrier Reef).

ISOPOD	HOST		DISTRIBUTION
A. apogonae	Apogonidae	*Apogon cooki*	northern and eastern Australia
		Apogon species	Palm Group, GBR
		Apogon fasciata	Moreton Bay
		Apogon cyanosoma†	Palm Group, GBR
		Cheilodipterus quinquelineatus	northern GBR
A. dimidiata	Nemipteridae	*Nemipterus** sp.	Gulf of Carpentaria
	Leiognathidae	*Leiognathus bindus*	eastern Queensland
A. leptosoma	Clupeidae	*Nematalosa come*	eastern Queensland
		Nematalosa erebi	southern Queensland
A. longicauda	Priacanthidae	*Priacanthus* sp.	GBR
	Haemulidae	*Plectorhynchus goldmani*	Swains Reefs, GBR
		Diagramma picta	North West Shelf; Lizard Island†, GBR
A. nemipteri	Nemipteridae	*Nemipterus virgatus*	North West Shelf
		*Nemipterus tolu**	Gulf of Carpentaria
		Scolopsis bilineatus	GBR
		Scolopsis margaritifer	Lizard Island, GBR
		Scolopsis monogramma	Palm Group, GBR
		Pentapodus setosus	Palm Group, GBR
	Pomacentridae	*Pomacentrus jerdoni*	North West Shelf
A. pomacentri	Pomacentridae	*Pomacentrus amboinensis*	Waining Reef, GBR
		Pomacentrus lepidogenys	Palm Group, GBR
		Pomacentrus melanochir	Lizard Is., GBR
		Pomacentrus melanopterus	Palm Group, GBR
		Pomacentrus moluccensis	Palm Group, GBR
		Pomacentrus pavo†	Lizard Is., GBR
		Chromis atripes	Carter Reef, GBR
		Chromis margaritifer	Myrmidon Reef, GBR
		Chromis nitidus	Capricorn Group, GBR
		Neopomacentrus violascens†	Palm Group, GBR

Key to Australian Species of *Anilocra*

1. Pereopods 2–4, or 1–4 with nodules on dactylus. 2

——Pereopods 1–4 without nodules on dactylus. 9

2. Antennule article 3 anterodistal margin produced. 3

——Antennule article 3 anterodistal margin not produced. 8

3. Pleonite 1 concealed by pereonite 7; uropod apices acute. ..... *A. koolanae*

——Pleonite 1 not concealed by pereonite 7; uropod apices rounded. 4

4. Pleotelson lateral margins flat or weakly turned up; pereopods 1–4 with 3 dactylus nodules. 5

——Pleotelson lateral margins upturned; pereopods 1–4 with only anterior dactylus nodule conspicuous. 7

5. Body about 4.0–4.5 times as long as wide; antennule article 3 strongly produced, 2.0 times as wide as long. ..... *A. alloceraea*

——Body less than 4.0 times as long as wide; antennule article 3 weakly produced, 1.2–1.4 times as wide as long. 6

6. Pleotelson ovate, lateral margins converging smoothly to caudomedial point; pleonite 1 lateral margin posteriorly produced. ..... *A. leptosoma*

——Pleotelson lateral margins weakly convex, posterior margin biconcave, distinct from lateral margin; pleonite 1 lateral margin not posteriorly produced. .... *A. caudata*

7. Antenna extending to posterior of pereonite 2; pleonite 5 dorsal posterolateral angle strongly produced, acute. ..... *A. dimidiata*

——Antenna not extending to posterior of pereonite 2; pleonite 5 dorsal posterolateral angle weakly produced. ..... *A. nemipteri*

8. Pereopod 1 dactylus without nodules; pleonites 4 and 5 dorsal posterolateral angles produced, acute; pleotelson posterior margin distinct from lateral margin. ..... *A. apogonae*

——Pereopod 1 dactylus with nodules; pleonite 5 only with dorsal posterolateral angle produced; pleotelson margins smoothl rounded. ..... *A. soelae*

9. Antennule article 3 anterodistal margin produced. 10

——Antennule article 3 anterodistal margin not produced. 11

10. Pleotelson ovate, widest medially; uropods not extending beyond posterior of pleotelson; pereopods 1–4 with short robust dactylus (Fig. 25A). .... *A. longicauda*

——Pleotelson widest anteriorly; uropods extending beyond posterior of pleotelson; pereopods 1–4 with long dactylus (Fig. 26K). ..... *A. ankistra*

11. Antenna extending to pereonite 3; body sub-parallel in shape; rostrum weakly developed. ..... *A. morsicata*

——Antenna extending to anterior of pereonite 2; body ovate in shape; rostrum distinct. ..... *A. pomacentri*

Anilocra alloceraea Koelbel

Figs 4, 5

Anilocra alloceraea Koelbel, 1878: 407, pl. 2, figs 1a-e.—Miers, 1880: 463.

Material examined. 11 females (ovig 20.0, 19.0, 18.0, 17.5, 17.0, non-ovig 17.5, 16.0, 15.5, 13.0), Batavia (=Jakarta), Indonesia, Dec 1928, op *Stolephorus indicus* (RMNH 1330). 3 females (ovig 21.0, 17.5, 17.0, non-ovig 18.0), Balikapan Harbour, East Kalimantan, Indonesia, 26 Aug 1976, from mangrove fishes (AM P36750). Female (ovig 22.0), off Orontes Reef, Arafura Sea, NT, 11°50.0′S, 132°04.3′E, 4 Aug 1986, trawled 20–24 m (NTM 4111).

Types. Some of Koelbel's (1878) other material is held at the Naturhistorisches Museum, Vienna, but of the specimens I have examined I have been unable to identify any types of *A. alloceraea*.

Type locality. Sumatra Sea (Koelbel, 1878).

Description of female. Body about 4.5 times as long as wide; dorsal surface smoothly domed. Pleonite 1 longest, posterolateral margins weakly produced; pleonites 2–4 subequal in length, posterolateral margins rounded; pleonite 5 with dorsal posterolateral margin acute, weakly produced. Pleotelson with lateral margins straight, upturned; posterior margin bisinuate, with broad caudomedial lobe, provided with short marginal setae.

Antennule not extending beyond posterior of eye, with 8 articles; article 3 with anterior margin strongly produced. Antenna extending to posterior of pereonite 1, with 10 articles, articles 2 and 3 obviously (about 0.6) narrower than article 1.

Mandible palp article 3 with about 11 setae on distal margin; article 2 medial margin weakly lobate. Maxillule with 4 terminal spines. Maxilla with 2 spines each on medial and lateral lobes respectively. Maxilliped article 3 with 3 terminal spines.

Pereopod 1 with large nodule on dactylus anterior margin, posterior margin with single nodule; pereopods 2–4 with prominent nodule on anterior margin, and 2 nodules on posterior margin of dactylus; nodules increasing in size from pereopods 2 to 4.

Pleopod rami slender, elongate (pleopod 1 exopod 2.5 times as long as wide; pleopod 2, 2.3; pleopods 3 and 4, 2.5); endopod of all pleopods shorter than exopod. Pleopods 3–5 with endopod proximomedial lobe prominent; pleopods 3 and 4 endopods each with small lobes; endopod of pleopod 5 massively folded. Uropod rami subequal in length, extending beyond posterior of pleotelson; distomedial margin of both rami with setae; exopod medial margin convex, lateral margin straight, apex narrowly rounded; endopod apex broadly rounded.

Male. Not known.

Colour. Pale creamy yellow, brown chromatophores over dorsal surfaces.

Size. Females 13.0–23.5 mm; Koelbel (1878) recorded his specimen at 29 mm.

Remarks. Miers (1880) first questioned the validity of *Anilocra alloceraea* suggesting that it could be a synonym of *A. leptosoma,* and later workers (Monod,

1934; Trilles, 1975) accepted this synonymy. There are numerous differences between the two species, several of which are clearly illustrated in Koelbel's (1878) figures. These are: the body 4.5 times longer than wide (*A. leptosoma,* 3.5); pleonite 1 long (short); lateral margins of pleotelson turned up (flat); posterior margin of pleotelson bisinuate with broad caudomedial lobe (smoothly curving to small caudomedial lobe); antennule article 3 strongly produced (moderately produced); pereopod 1 anterior nodule prominent (pereopod 1 nodule weak).

Anilocra caudata differs from *A. alloceraea* by having the pleotelson posterior margin acutely angled, pleotelson lateral margins weakly turned up, pleonite 1 short, antennule article 3 weakly produced, and a more ovoid body shape.

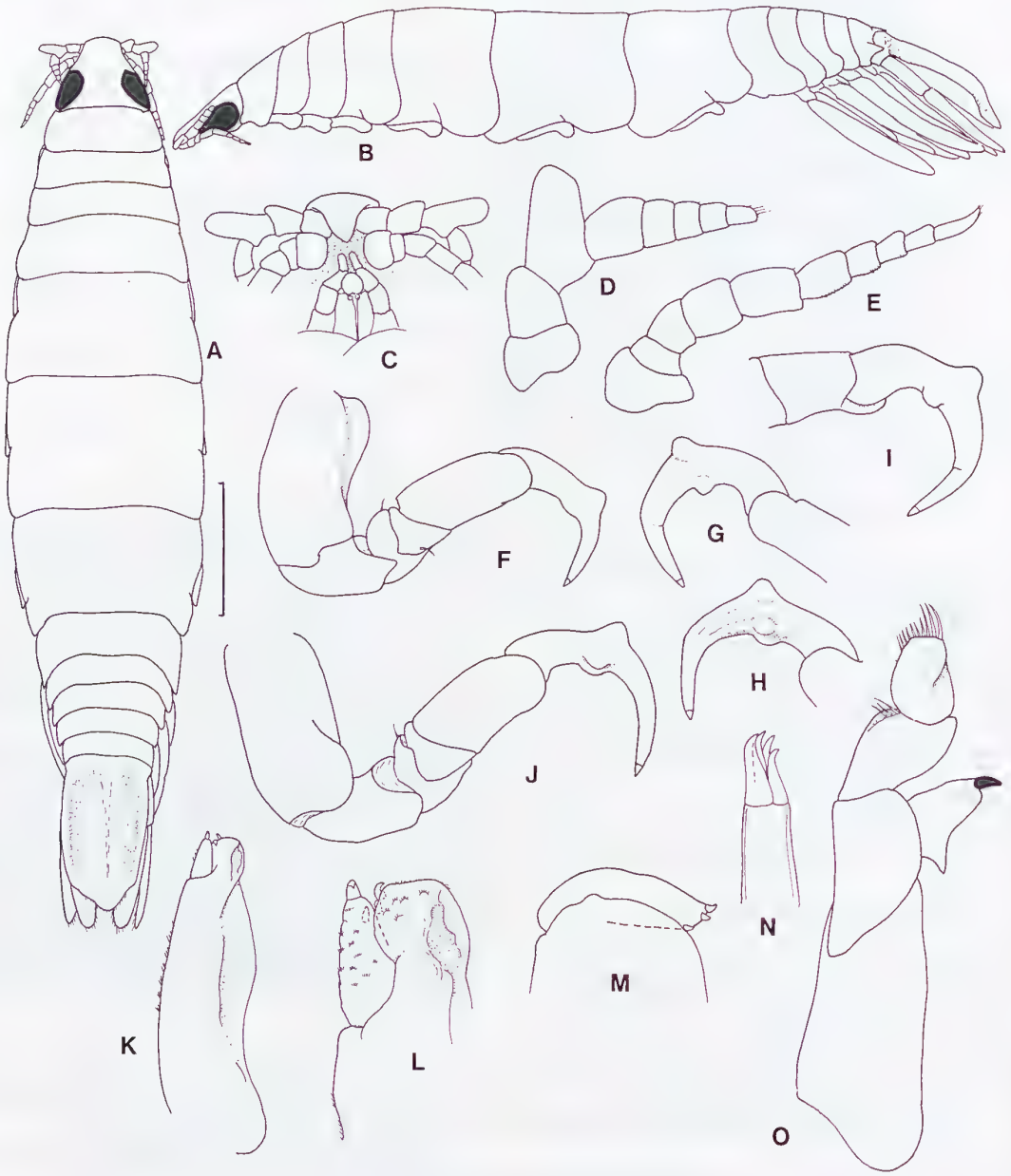

Fig. 4. *Anilocra alloceraea,* A–C, female 20.0 mm, remainder female 19.0 mm (RMNH 1330). **A,** dorsal view; **B,** lateral view; **C,** frons; **D,** antennule; **E,** antenna; **F,** pereopod 1; **G,** pereopod 4, dactylus, lateral view; **H,** pereopod 4, dactylus, posterior perspective; **I,** pereopod 4, dactylus, medial view; **J,** pereopod 2; **K,** maxilla; **L,** maxilla apex; **M,** maxilliped article 3; **N,** maxillule apex; **O,** mandible. Scale line represents 3.0 mm.

Hosts. Indonesian material recorded from *Stolephorus indicus* (F. Engraulidae).

Distribution. Jakarta, Indonesia; in Australia from Orontes Reef, Cobourg Peninsula, Northern Territory.

Anilocra cavicauda Richardson

Fig. 6

Anilocra cavicauda Richardson, 1910: 18, fig. 17.—Nierstrasz, 1931: 129. Not *Anilocra cavicauda*.—Hale, 1926: 210, fig. 7 (= *Anilocra nemipteri*).

Material examined. HOLOTYPE: Female (ovig 31.0), Pandanon Island, Philippines, 23 March 1909, coll. U.S. Bureau of Fisheries *Albatross* Philippine Expedition, 1907–1908 (USNM 40936).

Descriptive notes. Body about 3.4 times as long as wide. Pleonite 1 posterolateral margins not produced, pleonites 2–4 with posterolateral margins rounded; pleonite 5 with dorsal posterolateral margins acute. Pleotelson lateral margins weakly turned up, posterior margin tapering to narrowly rounded caudomedial point.

Antennule article 3 produced. Antenna extending to posterior of pereonite 1. Pereopods 1–4 with weakly developed nodule on dactylus anterior margin. Uropods extending to posterior of pleotelson, apices acute; exopod distinctly shorter than endopod.

Remarks. Monod (1934) included *A. cavicauda* in his synonymy for *A. longicauda,* this being later followed by Trilles (1975) although neither author gave their reasons. The figures given here for both species show that they cannot be considered conspecific, differing in numerous aspects of their morphology. *Anilocra cavicauda* has pereopod dactyli 1–4 with a nodule on the anterior margin, while in *A. longicauda* the pereopod dactyli lack nodules and are far shorter. Antennule article 3 of *A. cavicauda* is produced, and is not produced in *A. longicauda*. Lastly the figures given here illustrate the very different pleotelson shape of the two species.

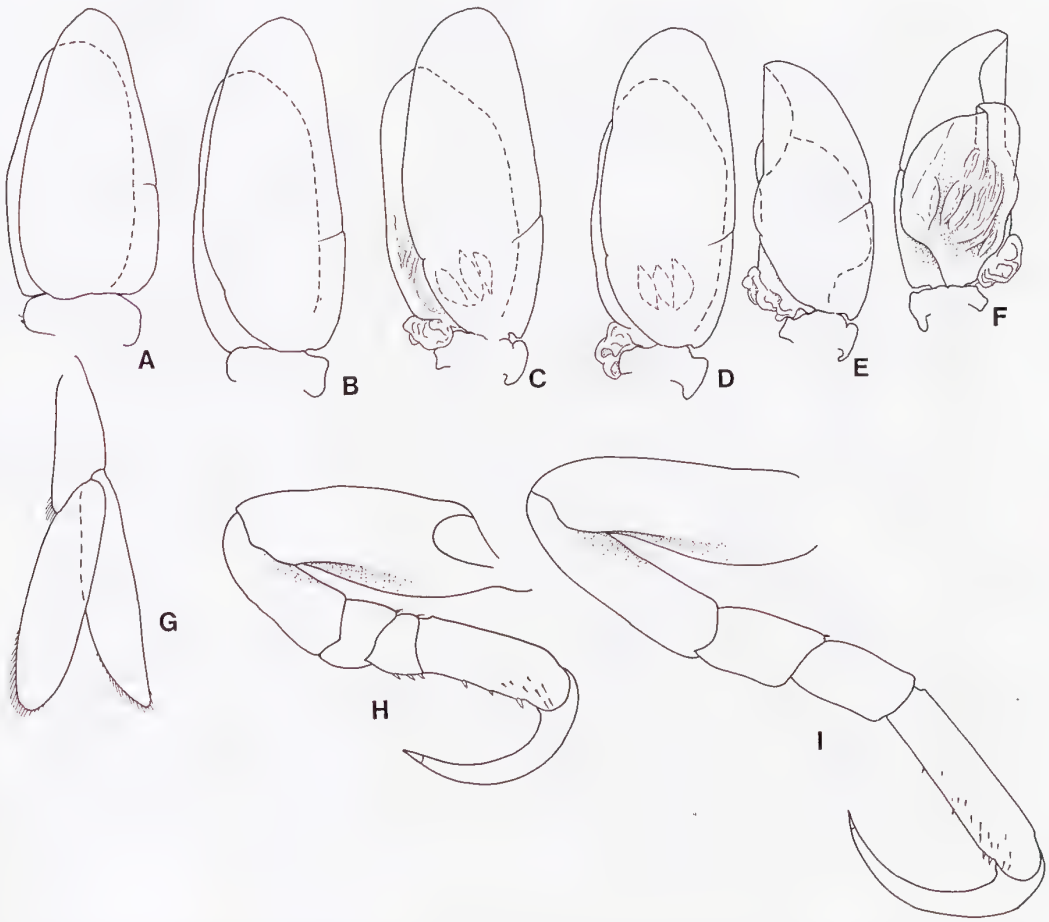

Fig. 5. *Anilocra alloceraea,* female, 19.0 mm (RMNH 1330). **A–E,** pleopods 1 to 5 respectively; **F,** pleopod 5, posterior view; **G,** uropod; **H,** pereopod 6; **I,** pereopod 7.

Hale (1926) recorded this species from Australia, but his record is a misidentification, the specimens being *A. nemipteri*.

Hosts. Not known.

Distribution. Philippines (Richardson, 1910).

Anilocra caudata Bovallius

Figs 7, 8

Anilocra leptosoma Bleeker, var. *caudata* Bovallius, 1887: 13, pl. III figs 29–38.

Anilocra leptosoma.—Monod, 1934: 11, pls 19, 22A, B, 23,

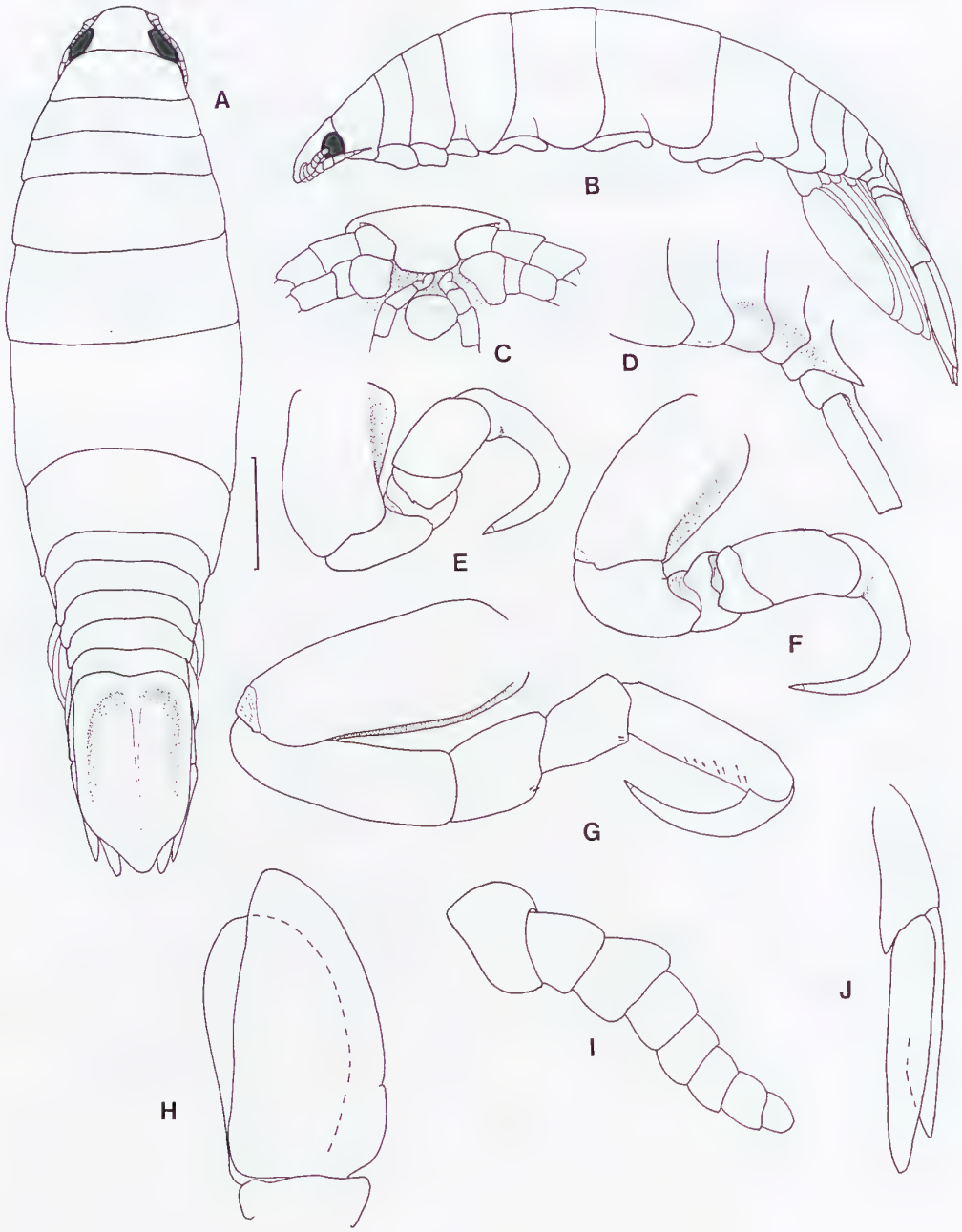

Fig. 6. *Anilocra cavicauda*, holotype (USNM 40936). **A**, dorsal view; **B**, lateral view; **C**, frons; **D**, pleon, lateral view; **E**, pereopod 1; **F**, pereopod 2; **G**, pereopod 7; **H**, pleopod 1; **I**, antennule; **J**, uropod. Scale line represents 4.0 mm.

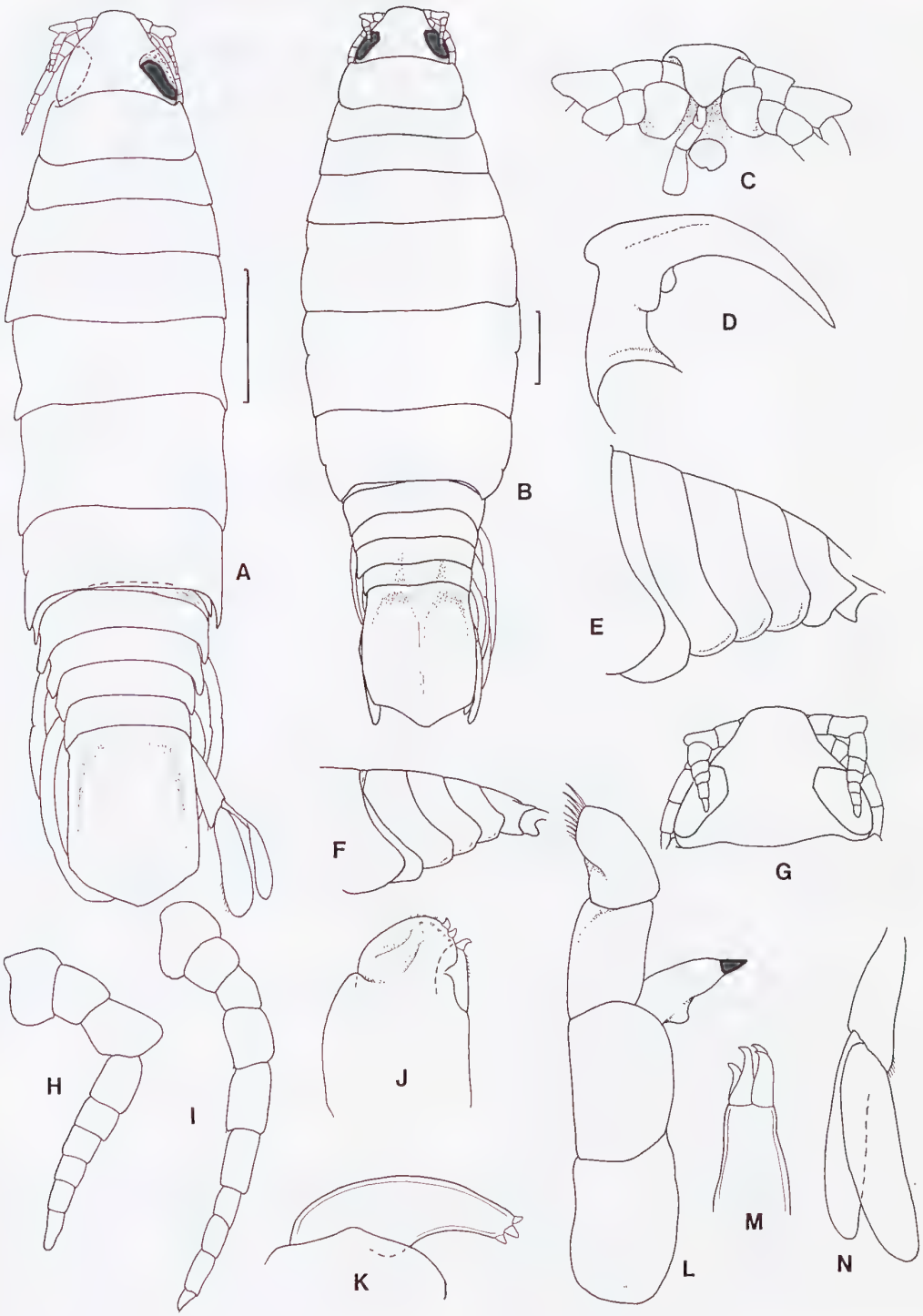

Fig. 7. *Anilocra caudata*, A, C, D, F, holotype (NRS 5774), remainder female (30.0 mm) NTM Cr 4240. **A**, dorsal view; **B**, dorsal view; **C**, frons; **D**, pereopod 2 dactylus, in situ; **E**, pleon, lateral view; **F**, pleon, lateral view; **G**, cephalon; **H**, antennule; **I**, antenna; **J**, maxilla apex; **K**, maxilliped article 3; **L**, mandible; **M**, maxillule apex; **N**, uropod. Scale lines represent 3.0 mm.

24B; Trilles, 1975: 310, pl. 1, fig. 6 (not *A. leptosoma* Bleeker).

Material examined. HOLOTYPE: female (ovig 21.0), Philippinerna, Wessel (NRS Is. 5774). Bovallius (1887) mentioned only the one specimen, held at the Rijksmuseum, Stockholm. The specimen is in very poor condition, and dissected appendages are missing.

Non-type: female (non-ovig 23.5), Snake Bay, Melville Island, NT, 11°25′S 130°41′E, Sept 1975, depth 60 m (NTM Cr2291). Female (ovig 30.0), North of Cape Wessel, NT, Arafura Sea, 10°24′S 133°36′E, 3 Feb 1985, depth 61 m, prawn trawl, coll. R. Williams (NTM Cr4240). Female (non-ovig 24.0), north of Wessel Islands, NT, 10°25′S 136°35′E, 1 Jan 1985, depth 64 m, coll. Rex Williams (NTM Cr4241). Female (ovig 31.0), south of Cooktown, Qld, 16°1′S 145°29′E, 6 Feb 1979, trawled, 20 m, coll. AM, AIMS (AM P36284).

Type locality. Philippines (Bovallius, 1887).

Description of Australian female. Body about 3.5 times as long as wide. Rostrum broad; eyes about 0.4 width of cephalon. Pleonite 1 short, largely concealed by pereonite 7, ventrolateral margins not posteriorly produced. Pleonites 2–4 with rounded lateral margins. Pleonite 5 dorsal posterolateral margins not produced. Pleotelson lateral margins straight, weakly turned up; posterior margin abruptly angled, forming distinct caudomedial point.

Antennule extending to posterior of cephalon; anterodistal margin of article 3 produced. Antenna with

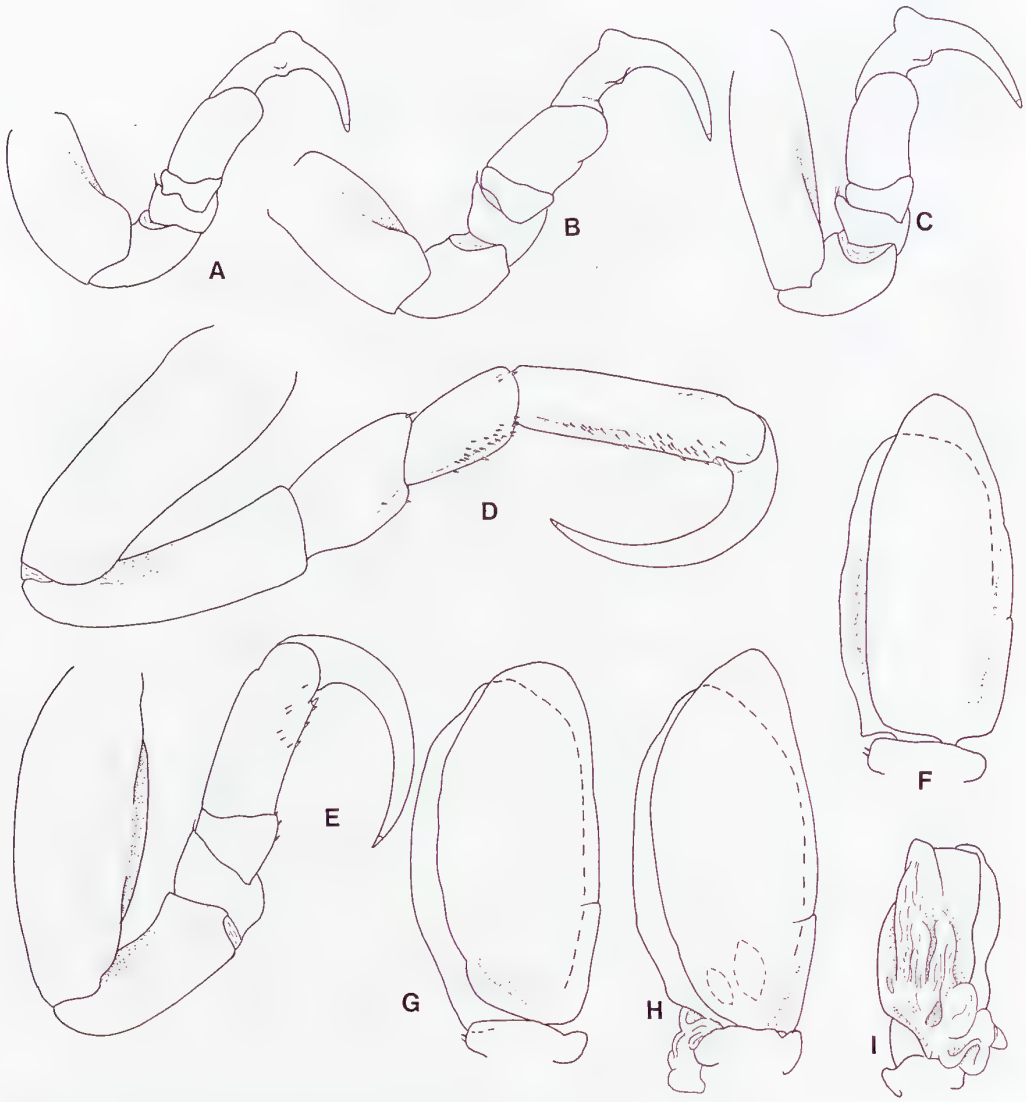

Fig. 8. *Anilocra caudata*, female (30.0 mm), NTM Cr 4240. **A**, pereopod 1; **B**, pereopod 2; **C**, pereopod 4; **D**, pereopod 7; **E**, pereopod 6; **F–I**, pleopods 1 to 3 and 5 respectively.

10 articles, extending to posterior of pereonite 1.

Mandible palp with about 10 setae on distolateral margin. Maxillule with 4 terminal spines. Maxilliped article 3 with 3 terminal spines.

Pereopod 1 with prominent nodule on dactylus anterior margin and 2 nodules on posterior margin; dactylus nodules increasing in prominence from pereopods 2–4. Pereopod 6 with 3 spines on propodal palm, about 6 spines on posteromedial surface. Pereopod 7 with abundant small spines on posterolateral margins of carpus and propodus.

Pleopods 1 and 2 elongate. Pleopod 3 endopod with prominent folded proximomedial lobe; endopod with 3 small folds; pleopod 4 with 3 small folds; pleopod 5 greatly folded. Uropod extending slightly beyond posterior of pleotelson, rami subequal in length, or exopod slightly shorter; apices broadly rounded.

Colour. Pale tan in alcohol.

Size. Females 21.0–30.0 mm.

Variation. The specimen from Melville Island has a more elongate body, about 4.5 times as long as wide, but otherwise agrees well with the other specimens.

Remarks. This species is most similar to *Anilocra leptosoma* and *A. monoma*. There are several differences between *A. leptosoma* and the material examined here, and Bovallius' (1887) subspecies is here given specific rank. The differences are in *A. caudata:* pleonite 1 posterolateral margins not produced (produced in *A. leptosoma);* pleotelson lateral margins straight, weakly upturned (convex and flat); pleotelson posterior margins abruptly angled to caudomedial point (converging smoothly to point).

Anilocra monoma has the pereopod nodules very weakly developed, and a pleotelson the same as that of *A. leptosoma. Anilocra cavicauda* differs from *A. caudata* in having more slender pleotelson and uropods, weakly developed pereopod nodules, and acute uropod apices.

Host. Not known.

Distribution. Vietnam (Monod, 1934), Philippines (Bovallius, 1887), Melville and Wessell Islands, Northern Territory, and off Cooktown, Queensland.

Anilocra dimidiata Bleeker

Figs 9, 10, 11

Anilocra dimidiata Bleeker, 1857: 21, 23, pl. 2, fig. 10.—Schiödte & Meinert, 1881: 111, pl. 8 figs 5, 6; Nierstrasz, 1915: 81; Monod, 1934: 10, pls 17C-D, 24A, 25D-F; Richardson, 1910: 18 (part).

Unconfirmed records or citations: Miers, 1880: 462; Gerstaecker, 1882: 261; Stebbing, 1900: 639; 1905: 26; Nierstrasz, 1918: 114; 1931: 128; Serène, 1937: 69; Pillai, 1954: 14; Trilles, 1975: 305, pl. 1 fig. 2; 1979: 249.

Anilocra carpentariensis Avdeev, 1977: 143, fig. 3.

Anilocra dimediata.—Bowman & Tareen, 1983: 5 (lapsus).

Material examined. SYNTYPES: 2 females (ovig 23.0, 25.0), Batavia (= Jakarta), Indonesia, coll. Bleeker (RMNH 22). Held at the Rijksmuseum van Natuurlijke Historie, Leiden.

Non-type: female (non-ovig 25.0), Baai van Batavia, 1910 (RMNH 21); female (ovig 26.0), Java Zee, April 1907, ex *Psettus evansi** (F. Monodactylidae, name unconfirmed) (RMNH 19); 5 females (ovig 20.0, 22.0, 24.0, non-ovig 23.0, 24.0), Batavia, Sept 1910, (RMNH 23); all from Indonesia, collected by P. J. Buitendijk, and reported on by Nierstrasz, 1915. 3 females (ovig 27.0, 21.0, non-ovig 22.0), Batavia, no other data (RMNH 1332). Numerous specimens, mostly juvenile (USNM 40968, 40969, 40971–73), Philippines, examined by Richardson (1910).

Australian material: female (non-ovig 10.5), Rargala Is., Wessel Islands, NT, 6 April 1982, commercial prawn trawl, coll. H.K. Larson (NTM Cr4242). 13 females [ovig 22.5 (AM P36277), 22.5, 22.0, 21.5 (AM P36279), 20.5, 20.5, 20.0, 20.0, 19.5, 19.5 (AM P36278), 18.5, non-ovig 21.5 (AM P36276), 18.0], Gulf of Carpentaria, 1969, from various trawled fishes *(Nemipterus*),* coll. CSIRO Gulf of Carpentaria Prawn Survey (AM P36275-P36279). Female (ovig 20.0), Cleveland Bay, Townsville, Qld, 3 Oct 1974, coll. D. M. Holdich (QM W10431). 2 females (non ovig 16.0, 17.5), Cleveland Bay, Townsville, Qld, 6 Sept 1983, ex *Equulites bindus,* coll. B. Ingram (QM W12176).

Type locality. Djakarta Bay (= Jakarta), Java, Indonesia (Bleeker, 1857).

Description of Australian female. Body 3.2–3.9 times as long as wide, coxae scarcely visible in dorsal view. Eyes large, about 0.46 width of cephalon; ocular surface shallowly domed. Pleon about 0.5 width of pereon; pleonite 1 longest, posterolateral margins not produced; posterolateral margins of pleonites 2–5 not produced; dorsal posterolateral angle of pleonite 5 strongly produced, acute, curving medially. Pleotelson lateral margins turned up; posterior margin bisinuate, with caudomedial lobe; lateral and posterior margin forming distinct angle.

Antennule with 6 or 7 articles, extending to posterior of eye; article 3 with anterodistal angle weakly produced. Antenna with 10 articles, extending to posterior of, or just beyond pereonite 2; articles 1–3 short, 5–10 elongate; posterior margins of articles 5–7 with blade-like edge.

Mandible palp with 4 setae on distolateral margin of article 2, with 17 setae on distal margin of article 3. Maxillule with 4 terminal spines. Maxilla with 2 spines each on medial and lateral lobe respectively.

Pereopods 1–4 with nodule on dactylus anterior margin progressively increasing in prominence, nodule on dactylus posterior margin very weak.

Pleopods prominent in dorsal view; pleopods 1 and 2 with suture on exopod lateral margin, and on both margins of exopods of pleopods 3–5. Pleopods 3–5 endopods with prominent proximomedial lobe. Pleopod 3 endopod without folded lobes, pleopod 4 with single small lobe, pleopod 5 endopod with 3 large folds. Uropod rami extending beyond posterior of pleotelson, both rami curving medially; exopod narrower and slightly shorter than endopod, peduncle mediodistal angle produced and acute.

Male. None examined.

Colour. Dense brown chromatophores on side that is uppermost when on host.

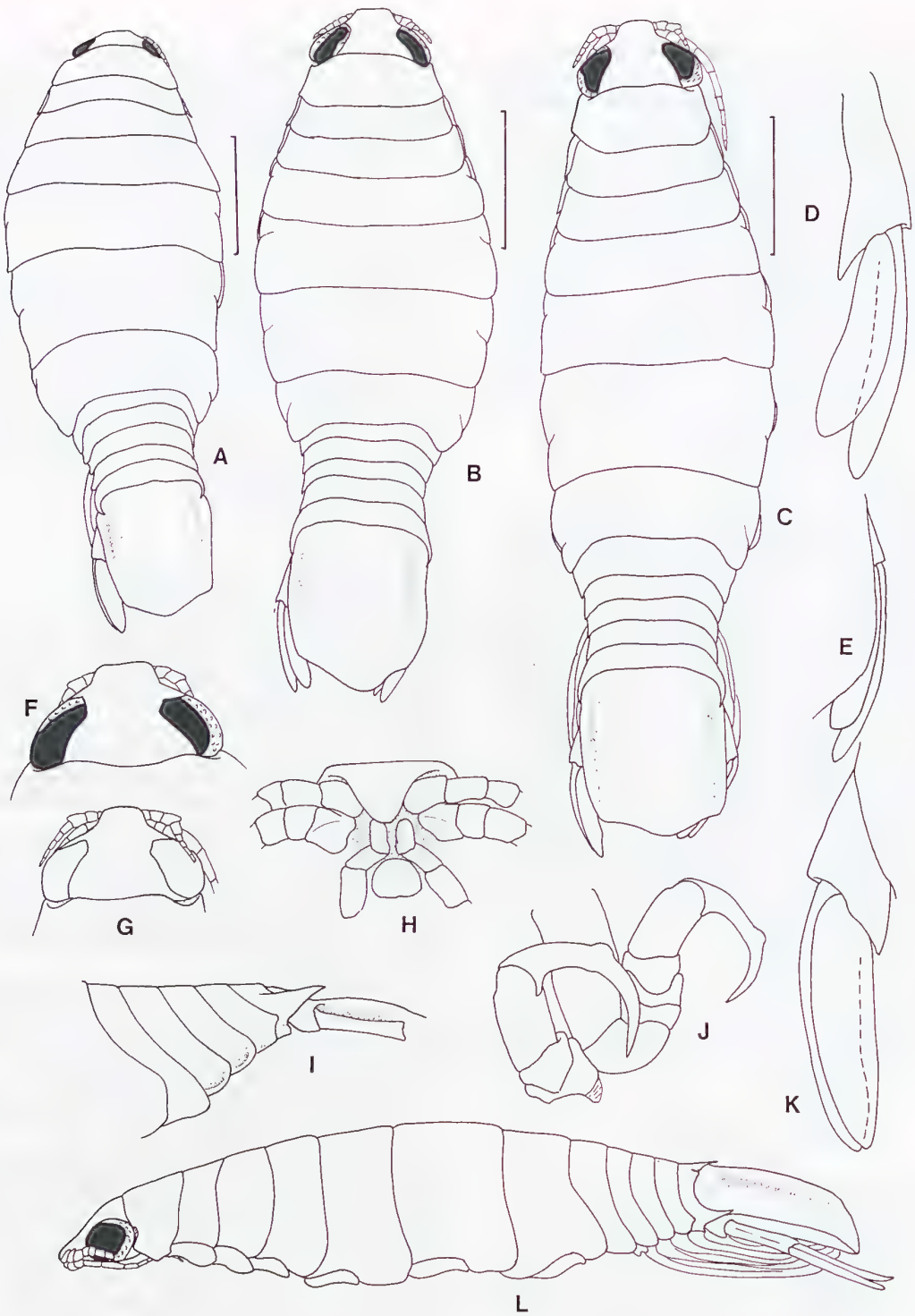

Fig. 9. *Anilocra dimidiata,* A, H–J, syntype, 25.0 mm; F, syntype 23.0 mm; remainder as indicated. **A,** dorsal view; **B,** female, AM P36276; **C,** female, AM P36277; **D,** uropod, female, AM P36279; **E,** uropod, female 27.0 mm, RMNH 1332; **F,** cephalon; **G,** cephalon, female, AM P36277; **H,** frons; **I,** pleon, lateral view; **J,** pereopods 1, 2, in situ; **K,** uropod, female 20.0 mm, RMNH 23; **L,** lateral view, female, AM P36277. Scale lines represent 4.0 mm.

Size. Ovigerous females 18.5–27.0 mm, non-ovigerous females 16.0–23.0 mm.

Variation. Indonesian specimens are generally wider than Australian specimens, but width ranges of the two populations overlap. In all Australian specimens the uropod exopod is longer and narrower than the endopod, while in Indonesian specimens the uropod rami are most commonly subequal in length.

Remarks. The strongly produced and acute posterolateral margins of pleonite 5, weakly produced antennule article 3, antenna extending to the posterior of pereonite 2, and weakly developed nodules on the posterior margin of the dactylus of pereopods 1–4 all serve to identify this species.

The types of *Anilocra carpentariensis* were not made available for study, but Avdeev's (1977) figures agree

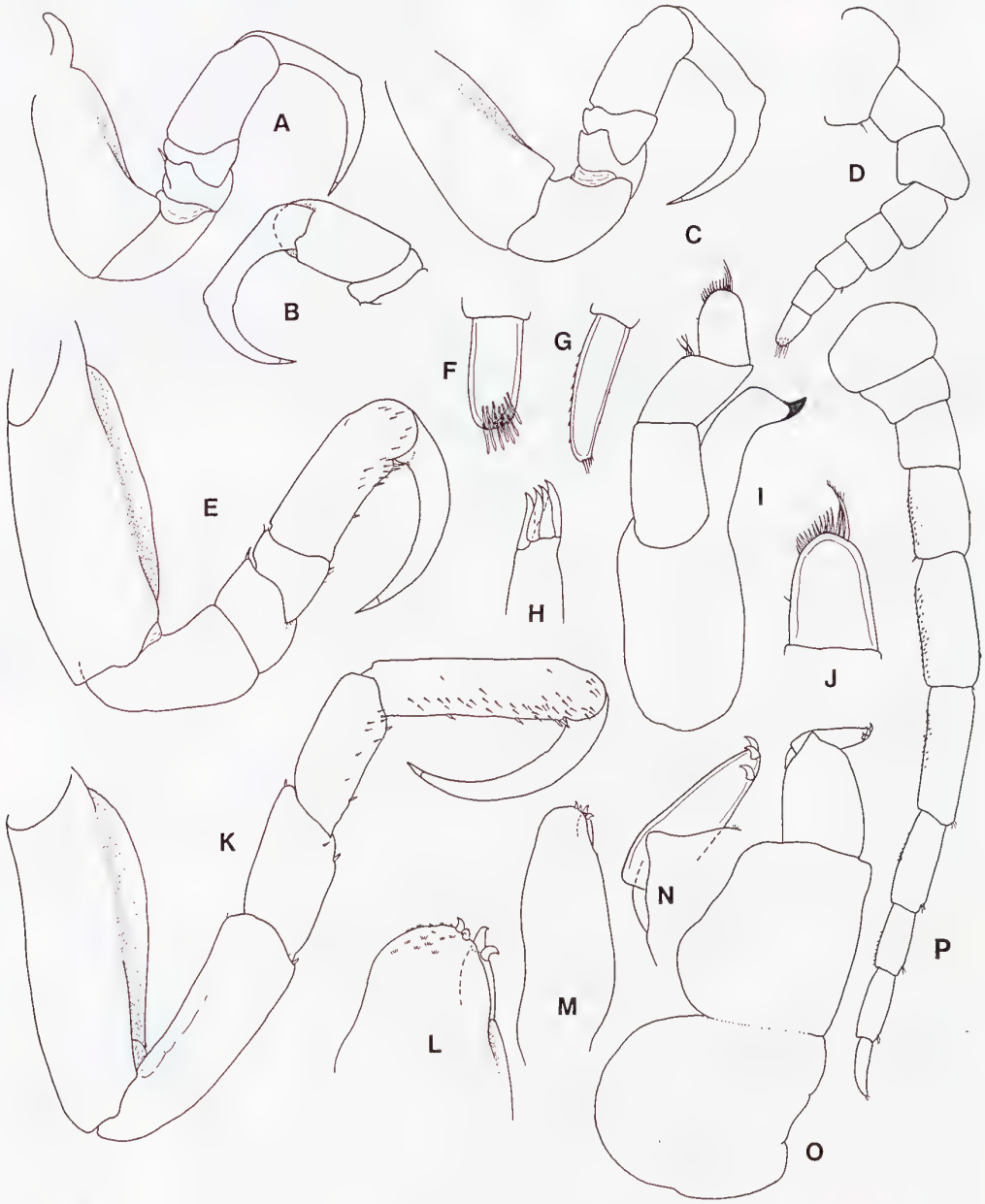

Fig. 10. *Anilocra dimidiata,* A–C, E, H–K, female, AM P36279, remainder female, AM P36276. **A,** pereopod 1; **B,** pereopod propodus, medial view; **C,** pereopod 2; **D,** antennule; **E,** pereopod 6; **F,** antennule apex; **G,** antenna apex; **H,** maxillule apex; **I,** mandible; **J,** mandible palp, article 3; **K,** pereopod 7; **L,** maxilla apex; **M,** maxilliped; **N,** maxilliped article 3; **O,** maxilliped; **P,** antenna.

with the characters listed above, and the species is here synonymised with *A. dimidiata.*

Hosts. *Psettus evansi** (Monodactylidae) (Nierstrasz, 1915); *Leiognathus bindus,* positioned dorsal to the eye; and unspecified *Nemipterus* spp.

Distribution. Indonesia; Vietnam (Monod, 1934); Philippines (Richardson, 1910). Wessell Islands, Gulf of Carpentaria and Townsville in Australia. The numerous unconfirmed records suggests that this species may have a wider distribution.

Anilocra leptosoma Bleeker
Figs 12, 13

Anilocra leptosoma Bleeker, 1857: 21, 30, pl. 1, fig. 6.—Schiödte & Meinert, 1881: 108, pl 8 figs 2–4.

Unconfirmed records or citations: Gerstaecker, 1882: 261; Stebbing, 1900: 640; 1905: 26; Nierstrasz, 1915: 87; 1931: 129; Monod, 1933: 196, fig. 62/3; Barnard, 1925: 392; 1936: 165, fig. 7c,d,e; Boone, 1935: 213, pl. 62; Serène 1937: 69; Pillai, 1954: 14; Kensley, 1978: 78, fig. 32C; Trilles, 1979: 248.

Not *A. leptosoma:* Monod, 1934: 11, pls 19, 22A, B, 23, 24B; Trilles, 1975: 310, pl. 1, fig. 6 (= *Anilocra caudata).*

Material examined. LECTOTYPE: female (ovig 27.0), Batavia (= Jakarta), Indonesia, coll. Bleeker (RMNH 30). Bleeker (1857) stated that he examined four specimens. At present only one specimen appears to be extant, and in some respects does not agree with Bleeker's figure. This specimen, as the only known type specimen for the species is here designated as lectotype.

Non-type: female (ovig 26.0), Philippines, Salmin (RMNH 4955) (examined by Schiödte & Meinert, 1881). From *Nematalosa come,* Qld: female (non-ovig 30.0), Cleveland Bay, Townsville, 19 March 1983, above left operculum (QM W12177); 2 females (ovig 32.0, non-ovig 24.0), Rose Bay, northern Qld, 23 May 1983, above left operculum (QM W12178); female (ovig 27.0), Townsville, 4 Oct 1983 (AM P36280); all coll. B. Ingram. Female (non-ovig 21.0), King Park, Beaver Rocks boat ramp, Mary River, south-east Qld, 10 April 1982, above and posterior to eye, coll. N.L. Bruce & E.J. Fields (QM W11005). Female (non-ovig 20.0), Cape Bowling Green, Northern Qld, 1914, ex *Dorosoma nasus** (name unconfirmed), coll. R. Hamlyn-Harris (QM W9481). Female (non-ovig 19.5), upper Brisbane River, south-east Qld, 7 Oct 1974, ex 'Bony Bream' *Fluvialosa erebi**, coll. R. Harrison (QM W4878).

Type locality. Djakarta, Indonesia (Bleeker, 1857).

Description of Australian female. Body about 3.3 times as long as wide. Dorsum domed, coxae just visible in dorsal view. Rostrum broad; eyes large, about 0.5 width of cephalon. Coxae narrow. Pleonite 1 short, ventrolateral margin produced; pleonites 2–5 subequal

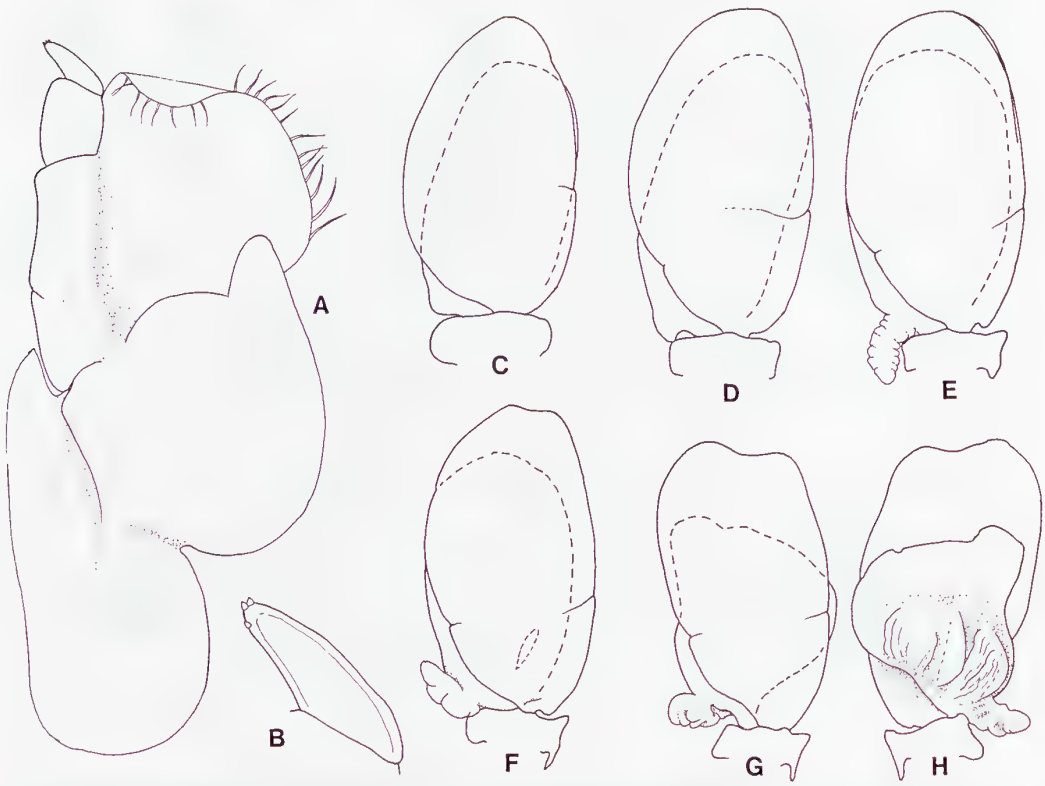

Fig. 11. *Anilocra dimidiata,* female, AM P36279. **A,** maxilliped; **B,** maxilliped article 3; **C–G,** pleopods 1 to 5 respectively; **H,** pleopod 5, posterior view.

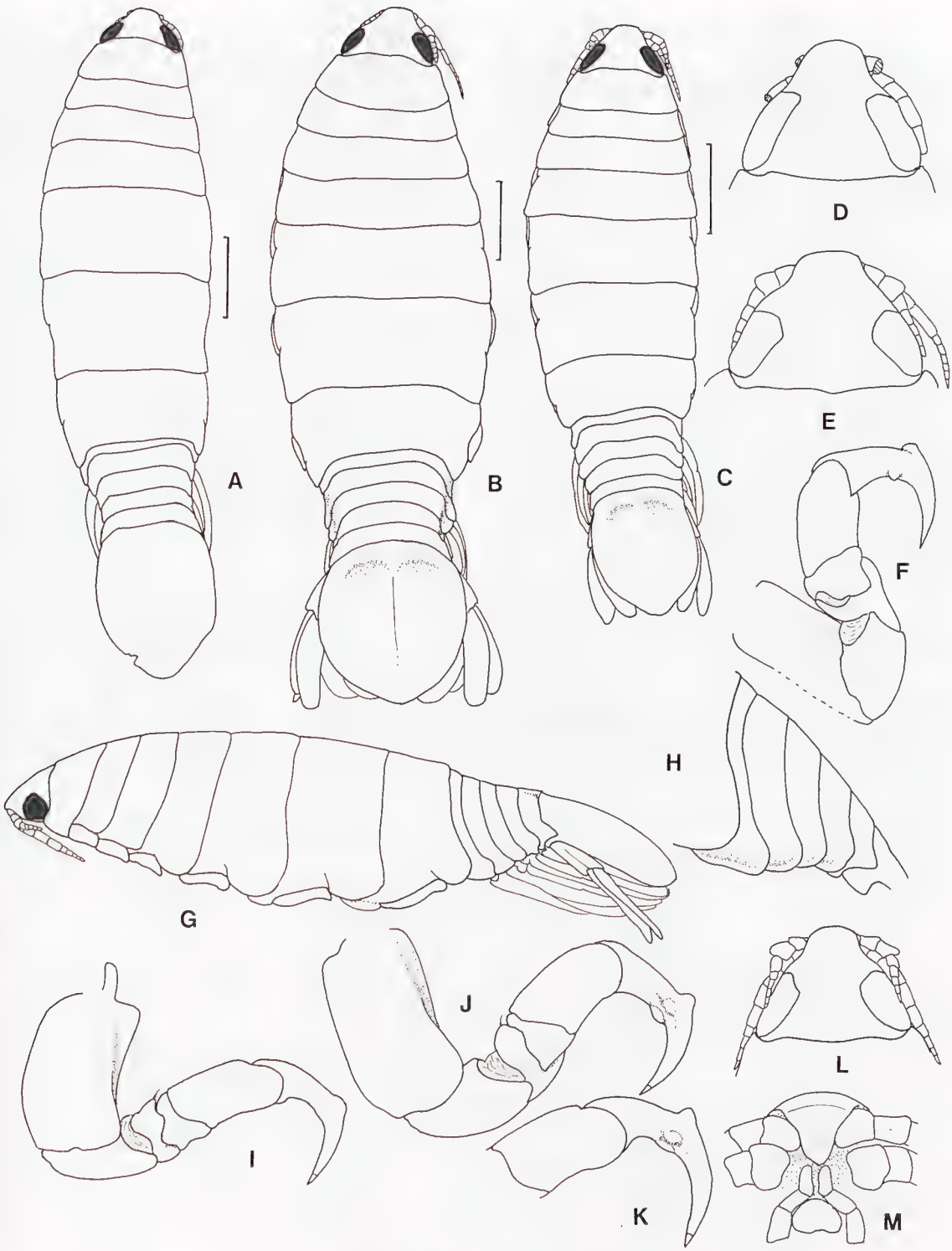

Fig. 12. *Anilocra leptosoma*. A, D, F, H, Lectotype RMNH 30; B, E, H, female 32.0 mm, Rose Bay; C, L, female 24.0 mm, Rose Bay; remainder female 27.0 mm (AM P36280). **A**, dorsal view; **B**, dorsal view; **C**, dorsal view; **D**, cephalon; **E**, cephalon; **F**, pereopod 2, in situ; **G**, lateral view; **H**, pleon, lateral view; **I**, pereopod 7; **J**, pereopod 2; **K**, pereopod 4, dactylus; **L**, cephalon; **M**, frons. Scale lines represent 4.0 mm.

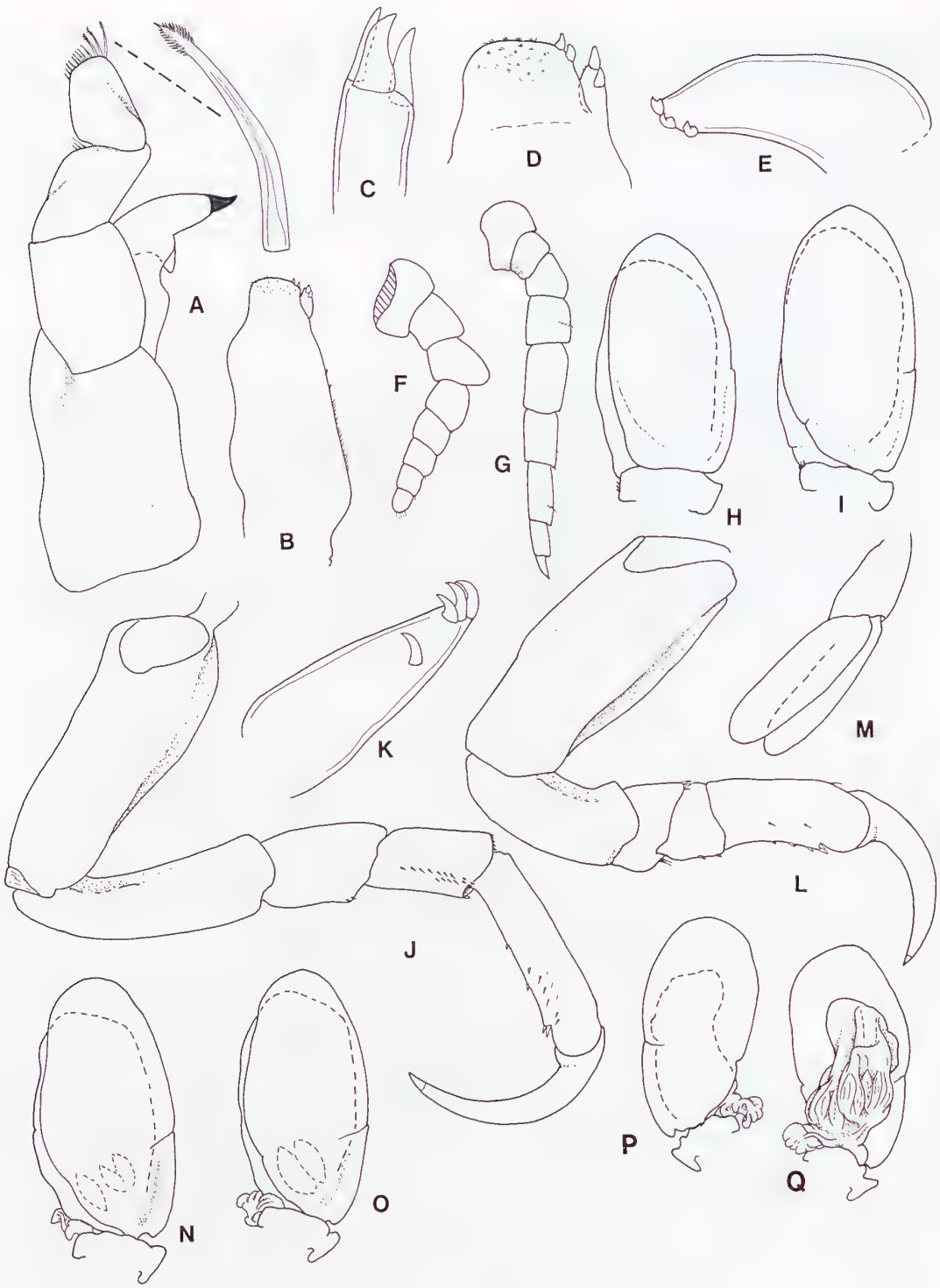

Fig. 13. *Anilocra dimidiata.* All figures female 27.0 mm (AM P36280) except where indicated. **A**, mandible; **B**, maxilla; **C**, maxillule apex; **D**, maxilla apex; **E**, maxilliped article 3; **F**, antennule; **G**, antenna; **H**, pleopod 1; **I**, pleopod 2; **J**, pereopod 7; **K**, maxilliped article 3, female 30.0 mm, Cleveland Bay; **L**, pereopod 6; **M**, uropod; **N–P**, pleopods 3 to 5; **Q**, pleopod 5, posterior view.

in length; lateral margins of pleonites 2–4 not produced; pleonite 5 dorsal posterolateral margins weakly produced. Pleotelson lateral margins convex, converging smoothly to medial point; lateral margins not folded up. Anterodorsal depression and mediolongitudinal ridge weakly developed, latter scarcely evident.

Antennule with 8 articles, extending slightly beyond midpoint of eye; anterodistal angle of article 3 strongly produced. Antenna with 9 articles, extending to middle or posterior of pereonite 2.

Maxilla medial lobe small. Mandible palp with 13 brush-tipped setae on distal margin of article 3. Maxilliped article 3 with 3 terminal spines.

Pereopod 1 dactylus with nodule on anterior margin, that of posterior margin scarcely developed. Pereopods 2–4 similar to 2, but increasing in length towards posterior; dactylus nodules prominent, anterior nodule large, proximal side steeply inclined, distal side gently inclined; posterior margin with 2 small nodules.

Endopods of pleopod 3 and 4 with 2 small folds; pleopod 5 endopod highly folded. Uropod peduncle about half length of endopod; exopod slightly shorter than endopod, apices of both rami rounded.

Male. Not known.

Colour. Pale tan to brown in alcohol; chromatophores over dorsal surface.

Size. Ovigerous females 26.0–32.0 mm, non-ovigerous females 21.0–24.0 mm.

Variation. In some specimens the uropod exopod apex is subacute. All Australian material accords well with the lectotype. Non-ovigerous female has 4 long spines on maxilliped article 3.

Remarks. Characters which serve best to identify this species are antennule article 3 being only moderately produced, pleonite 1 short, posterolateral corners of pleonites 4 and 5 not produced, flat and markedly ovate pleotelson with a distinct apex (occasionally forming a caudomedial lobe), rounded uropods, pereopod 1 with moderate nodules, and pereopods 2–4 with prominent anterior nodule and 2 posterior nodules.

Anilocra monoma is very similar, and can be separated only by the pereopod nodules being far less strongly developed, and the ventrolateral margins of pleonite 1 not posteriorly produced. Examination of the types of *A. monoma* showed one specimen had 2 weak nodules on the posterior margin of the dactylus of pereopod 3, as in *A. leptosoma* (see Fig. 14).

Anilocra alloceraea Koelbel, had long been considered a synonym of *A. leptosoma*. Comparison of Indonesian material to Koelbel's figure readily identified the species, and it can be distinguished from *A. leptosoma* by the far narrower body, far more strongly produced antennule article 3, more strongly developed nodules on the dactyls of pereopods 1–4, pleonite 1 being much longer, and pleotelson lateral margins strongly turned up with the posterior margin bisinuate.

Hosts. In Australia recorded from *Nematalosa come,* in marine waters, and *Nematolosa erebi* estuarine waters.

Distribution. Recorded from the Philippines (Schiödte & Meinert, 1881), Indonesia (Bleeker, 1857) and eastern Australia from Townsville to Brisbane.

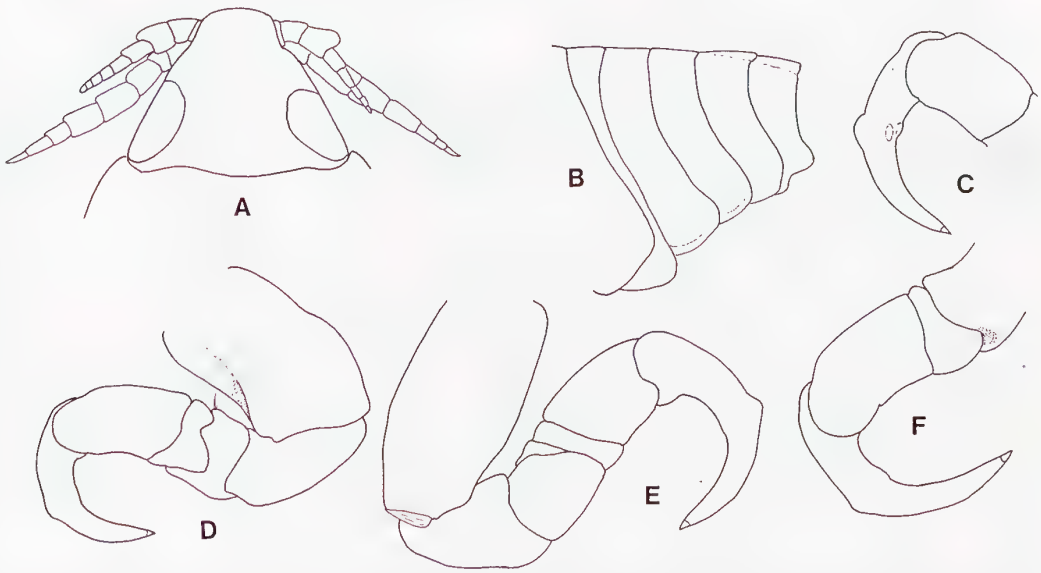

Fig. 14. *Anilocra monoma,* holotype (USNM 190881). **A,** cephalon; **B,** pleon, lateral view; **C,** pereopod 3 dactylus, perspective; **D,** pereopod 1; **E,** pereopod 3; **F,** pereopod 4.

Anilocra nemipteri n. sp.

Figs 15, 16, 17

Anilocra cavicauda.—Hale, 1926: 210, fig. 7; Beumer, et al., 1982: 31, 58 (not *A. cavicauda* Richardson, 1910).

Material examined. HOLOTYPE: female, (29.0 ovig), Northwest Shelf, WA, 18°54′S, 118°12′E, 6 June 1983, ex *Nemipterus virgatus*, silty sand bottom, coll. G.C.B. Poore & H.M. Lew Ton on FRV *Soela* (NMV J12947).

PARATYPES: 35 females [ovig 31.0 (NMV J12948), 22.5 (NMV J12950), 21 unmeasured, non-ovig 28.5 (NMV J12949), 25.0 (NMV J12951), 11 unmeasured], same data as holotype (NMV J11181). Female (ovig 27.5), near Mornington Island, Gulf of Carpentaria, Qld, 16°51′S, 139°51′E, 24 Jan 1983, 15 m, coll. C. Jones, QFS (QM W11335). Female (ovig 20.5), Torres Strait Prawn Survey, 1983, QFS (QM W10845). Lizard

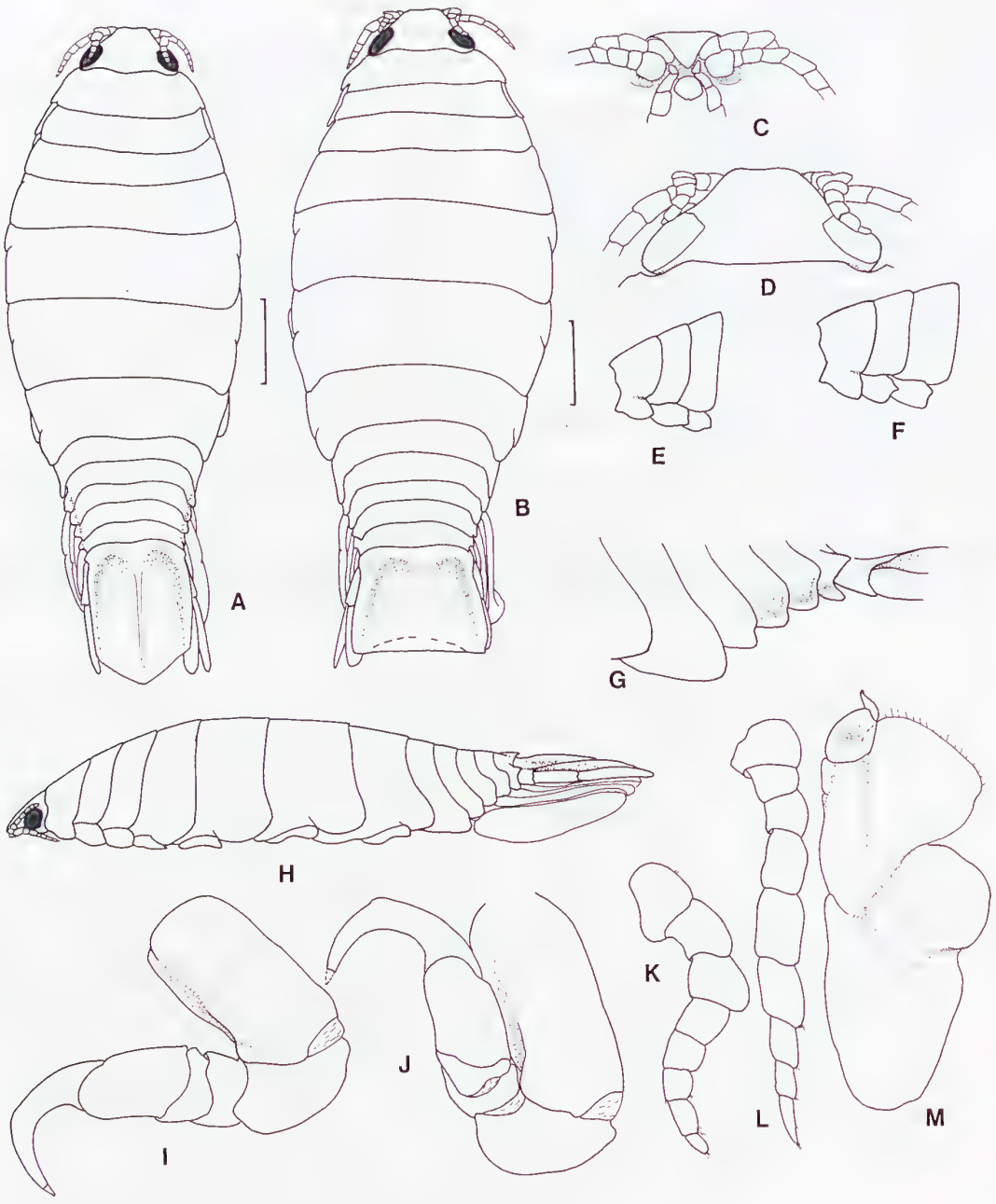

Fig. 15. *Anilocra nemipteri* n. sp., A, C, G, H, holotype; F, female #3, remainder female #1 (NMV J11181). **A**, dorsal view; **B**, dorsal view; **C**, frons; **D**, cephalon; **E**, anterior pereonites; **F**, anterior pereonites; **G**, pleon; **H**, lateral view; **I**, pereopod 1; **J**, pereopod 2; **K**, antennule; **L**, antenna; **M**, maxilliped. Scale lines represent 4.0 mm.

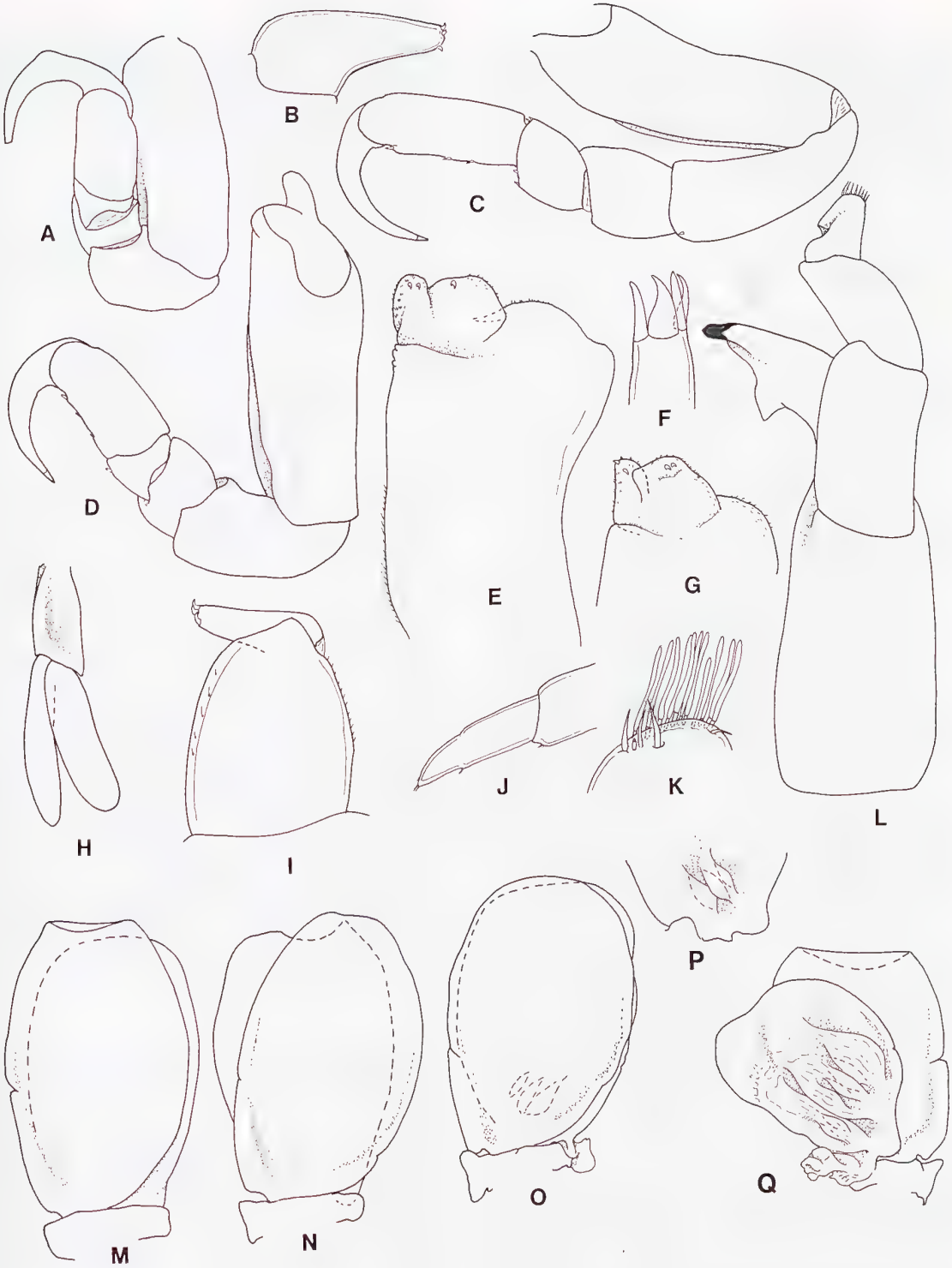

Fig. 16. *Anilocra nemipteri* n. sp., G, I, female #3, remainder female #1 (NMV J11181). **A,** pereopod 3; **B,** maxilliped article 3; **C,** pereopod 7; **D,** pereopod 6; **E,** maxilliped; **F,** maxillule apex; **G,** maxilla apex; **H,** uropod; **I,** maxilliped; **J,** antennule, terminal article; **K,** antenna, terminal article detail; **L,** mandible; **M–O,** pleopods 1 to 3 respectively; **P,** pleopod 3 endopod, posterior lobes; **Q,** pleopod 5, posterior view.

Island, Qld, northern Great Barrier Reef series – from *Scolopsis bilineatus:* female (damaged, ovig 19.0), Osprey Is., 15 July 1985, 15 m (AM P36254); male (7.0), Granite Bluffs, Lizard Island, 20 July 1985, 7 m (AM P36256); 3 females (ovig 22.0, non-ovig 13.0, immature 8.0), Osprey Is., 22 July 1985, from 3 hosts, 5 m (QM W12179); 2 females (ovig 23.0, 22.0), northern end of Granite Bluffs, Lizard Island, 23 July 1985, 2 hosts, 7 m (AM P36255); female (ovig 21.5), north-west side of Palfrey Is., 24 July 1985, 8 m (QM W12180); female (ovig 22.0), patch reef in front of Research Station, Lizard Island, 24 July 1985, 2 m (AM P36253); from *Scolopsis margaritifer:* 2 males (9.0, 7.5), north-west side of Palfrey Is., 23 July 1985, 2 hosts, 7 m (AM P36257); male (6.0), north-west side of Palfrey Island, 24 July 1985, 8 m (AM P36252); all coll. N.L. Bruce & R.T. Springthorpe.

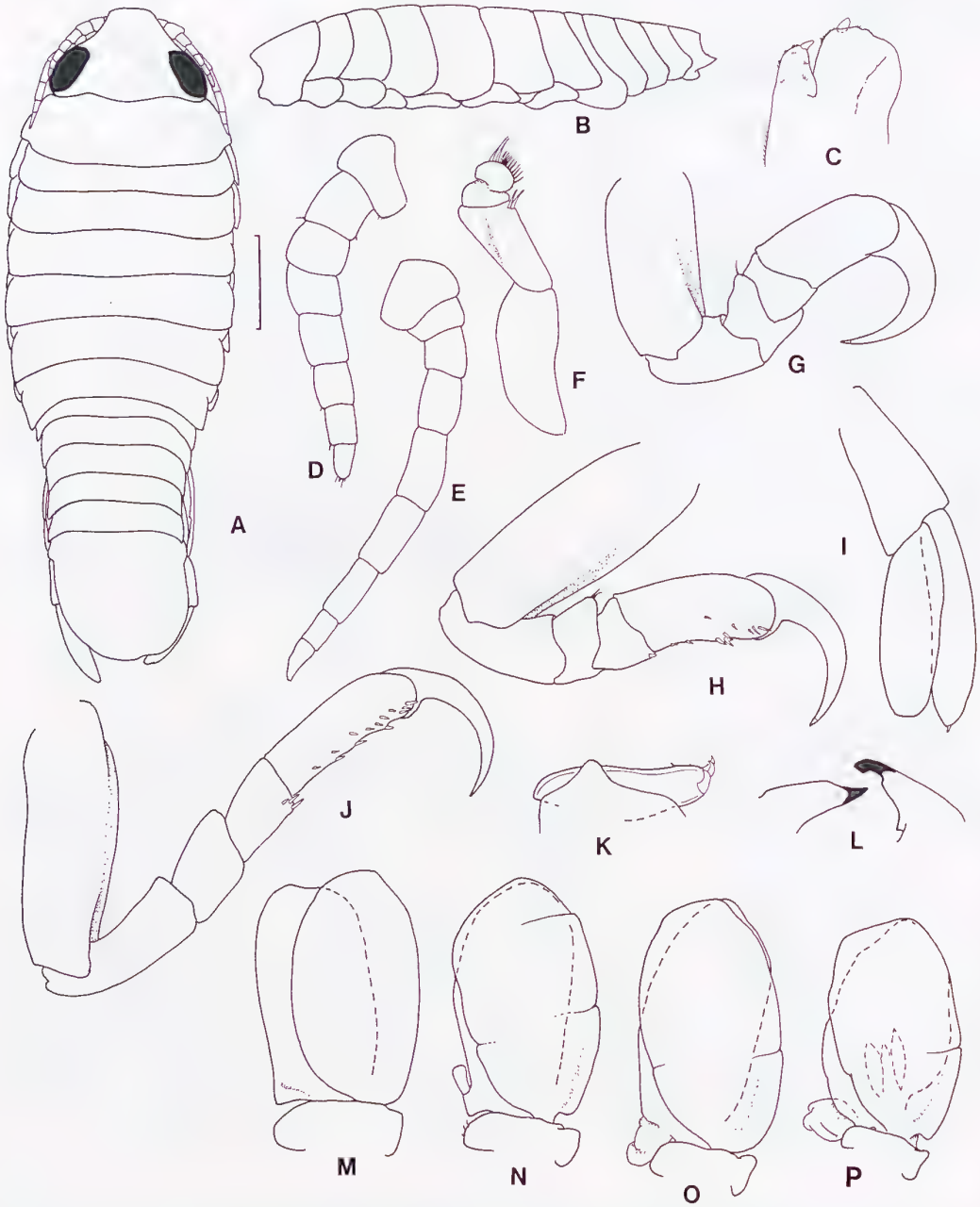

Fig. 17. *Anilocra nemipteri* n. sp., male 7.0 mm, Lizard Is. (AM P36256). **A**, dorsal view; **B**, pereon, pleon, lateral view; **C**, maxilla apex; **D**, antennule; **E**, antenna; **F**, mandible palp; **G**, pereopod 1; **H**, pereopod 6; **I**, uropod; **J**, pereopod 7; **K**, maxilliped article 3; **L**, right and left mandible incisors respectively; **M–P**, pleopods 1 to 3, 5 respectively. Scale line represents 1.0 mm.

Additional material. Two females, Northwest Shelf, WA, 19°58.7′S 117°00′E, 26 Oct 1983, depth 40 m, coll. T. Ward (NTM Cr4243). 10 females, Northwest Shelf, WA, 20°24.6′S 116°13.0′E, 9 June 1983, ex *Pristotis jerdoni,* 36 m, shelly sand bottom, coll. G.C.B. Poore & H.M. Lew Ton on FRV *Soela* (NMV J11182). Female, N.N.E. of Montebello Is., WA, 19°44′S 116°02′E, 3 March 1979, depth 105 m, coll. L.L. Marsh & S. Slack-Smith on FRV *Soela* (WAM 602-85). Female, east of Montebello Is., WA, 20°30′S 116°00′E, 2 Dec 1979, depth 37.5 m, coll. S. Slack-Smith & L. Marsh on FRV *Soela* (WAM 606-85). Female, south-western coast of Hermite Island, Montebello Is., WA, 12 Dec 1979, dredged 6 m, L. Marsh & S. Slack-Smith on FRV *Soela* (WAM 605-85). Female, 142 km north of Cape Lambert, WA, 19°06′S 117°17′E, 1 Oct 1982, depth 156 m, coll. L. Marsh on FRV *Soela* (WAM 601-85). 8 females, CSIRO Gulf of Carpentaria Prawn Survey, Qld, 30 Nov 1963, from *Odontoglossus tolu**, coll. D. F. McMichael (AM P36281). 8 females, CSIRO Gulf of Carpenataria Prawn Survey, Qld, Dec 1963, no other data, coll. J.C. Yaldwyn & D.F. McMichael (AM P36282). 7 females, CSIRO Gulf of Carpentaria Prawn Survey, from various trawled fishes *(Nemipterus*),* no other data (AM P36283). 2 females, (ovig 31.0, 29.0), Gulf of Carpentaria Prawn Survey, 6 Oct 1964, coll. R.W. George on *Rama* (WAM 597-85). Female, north side of Clack Reef, Qld, 14°03′S 144°15′E, 24 Feb 1979, ex *Scolopsis bilineatus,* coll. AIMS, QM, AM (QM W8937). Female (ovig 17.5), north-eastern point, Fantome Island, Palm Group, Qld, 20 April 1986, 18 m, on *Pentapodus setosus,* coll. N.L. Bruce, R.T. Springthorpe (AM P36747). Male (7.0), 19 Apr 1986, on *Scolopsis monogramma,* all data as previous (AM P36748).

Type locality. North West Shelf, WA, 18°54′S, 118°12′E.

Description of female. Body 2.4–3.0 times as long as wide, lateral margins convex in dorsal view. Rostrum not abruptly narrowed, anterior margin medially indented. Eyes about 0.3 width of cephalon. Pleonite 1 longest, posterolateral margin indented, then posteriorly produced; posterolateral margins of pleonites 2–4 very thin; dorsal posterolateral angles of pleonite 5 not produced. Pleotelson lateral margin bent dorsally, posterior margin abruptly angled with wide caudomedial lobe.

Antennule extending to midpoint of eye, with 8 articles, anterodistal margin of article 3 produced. Antenna extending to middle of pereonite 1, with 10 articles.

Mandible palp article 3 folded, with 9 terminal setae. Maxillule with 4 terminal spines. Maxilla medial lobe with 2 small spines, lateral with 1. Maxilliped article 3 with terminal spines.

Pereopods robust; nodule present on dactylus of pereopods 1–4, weakly developed on pereopod 1 distinct on pereopods 2 to 4. Pereopods 6 and 7 each with spine on posterodistal angle of carpus and 3 spines on posterior margin of propodus.

Pleopods broadly rounded; endopods of pleopods 3 and 4 with 3 small lobes, endopod of pleopod 5 with 3 large folded lobes; proximomedial lobe of pleopods 3–5 endopods prominent and folded. Uropods not extending beyond posterior of pleotelson, rami subequal in length, endopod wider than exopod.

Male. Rostrum not indented. Pleonite 1 posterolateral margin weakly produced. Pleotelson posterior margin evenly rounded, lateral margins not turned up. Antennule article 3 not produced. Mandible assymmetrical, right incisor acute, left blunt. Pereopods 1–4 without nodules on dactylus; pereopods 6 and 7 with propodus more spinose than female. Pleopod folding weakly developed.

Colour. In life, densely covered by chromatophores; on *Scolopsis bilineatus* and *S. margaritifer* appearing very dark brown; pale tan on *S. monogramma* and *Pentapodus setosus.* Preserved specimens vary from pale tan to dark brown.

Size. Ovigerous females 19.0–31.0 mm, non-ovigerous females 13.0–28.5 mm; males 6.0–9.0 mm.

Variation. Body width varies from 2.4–3.0 times as long as wide. The folding on the endopods of pleopods 3 and 4 is less developed in non-ovigerous and small specimens under about 25 mm. The shape of the posterior margin of the pleotelson is frequently irregular, often appearing damaged.

Specimens from *Pristotis jerdoni* are smaller in size (ovigerous females measuring 16.5–21.0 mm), have the posterolateral margins of pleonite 5 slightly more acute, and lack the indentation at the posterolateral margin of pereonite 1.

Specimens from *Scolopsis bilineatus* taken at Lizard Island are consistently wider than those from *Nemipterus,* but are otherwise identical.

Remarks. This species can be recognised by the broad ovate body shape, short antennule and antenna, weakly developed pereopod nodules on the dactylus anterior margin, and pleonite 1 long with posteriorly directed posterolateral margins.

Hosts. *Nemipterus virgatus, N. tolu*, Scolopsis bilineatus, S. margaritifer, S. monogramma, Pentapodus setosus, Pristotis jerdoni.* On nemipterids at Lizard Island and the Palm Group, there was only ever one isopod per host, always attached above and slightly posterior to the eye.

Distribution. North West Shelf of Western Australia, Gulf of Carpentaria, Torres Strait; Lizard Island and Palm Group of the Great Barrier Reef.

Etymology. The name is derived from that of the most common host genus.

Anilocra soelae n. sp.

Figs 18, 19

Material examined. All North West Shelf, WA, collected by FRV *Soela.* HOLOTYPE: female, (ovig 16.0), 19°03.5′S 119°03.6′E, 28 April 1983, depth 80 m, coll. A.J. Bruce (NTM Cr4244).

PARATYPES: 3 females (15.5, 15.5, non-ovig 14.0), same data as holotype (NTM Cr4244). Female (ovig 15.5), 18°56.8′S 118°45.2′E, 7 Dec 1982, depth 86 m, coll. T. Ward (AM P36272). Female (ovig 15.0), 19°44.0′S 117°54.6′E, 20 Sept 1983, depth 56 m, coll. T. Ward (AM P36271).

Type locality. North West Shelf, Western Australia, 19°03.5′S 119°03.6′E.

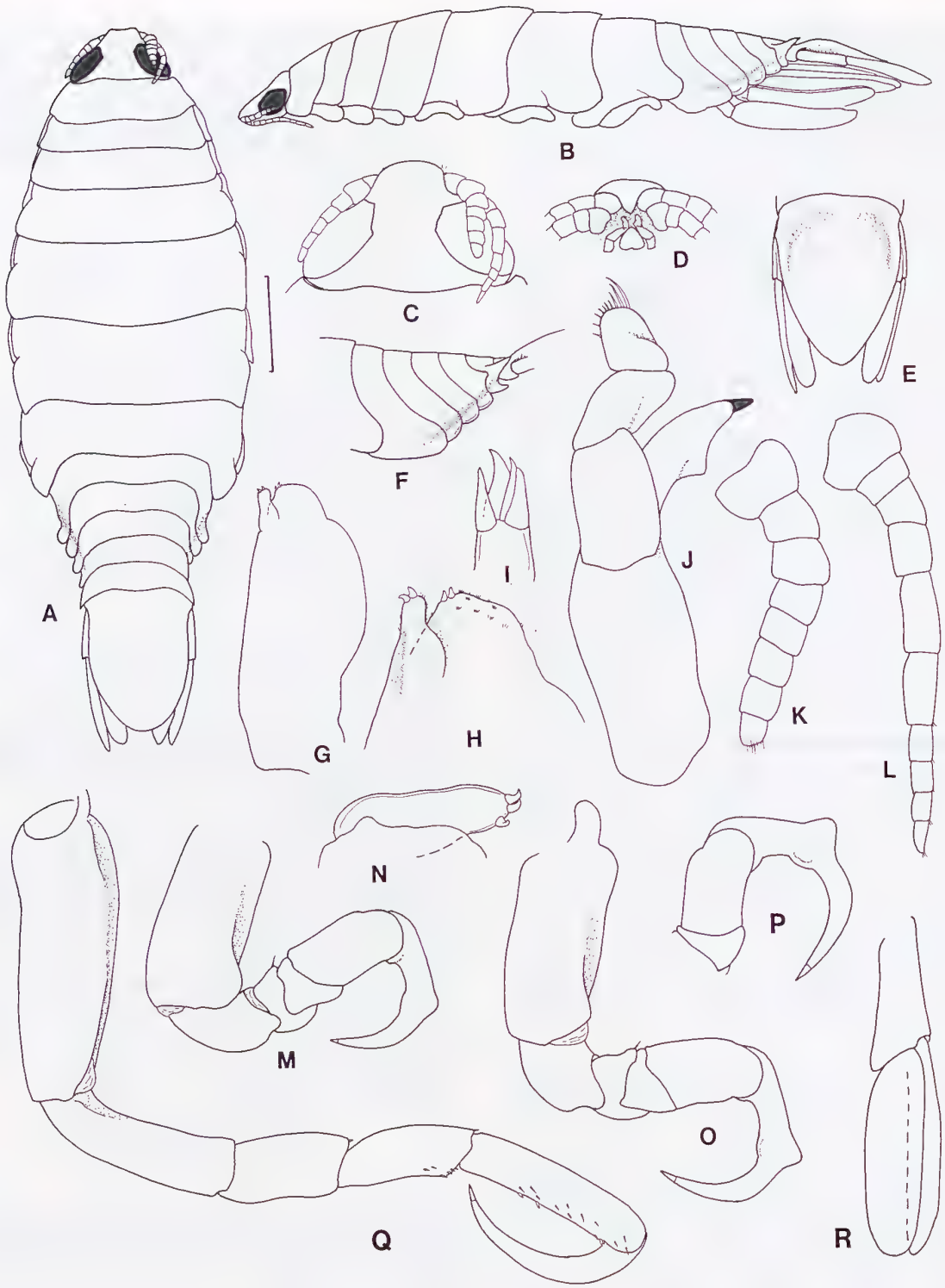

Fig. 18. *Anilocra soelae* n. sp., A–D, holotype, remainder female 15.5 mm (NTM Cr4244). **A**, dorsal view; **B**, lateral view; **C**, cephalon; **D**, frons; **E**, pleotelson, perpendicular view; **F**, pleon, lateral view; **G**, maxilla; **H**, maxilla apex; **I**, maxillule apex; **J**, mandible; **K**, antennule; **L**, antenna; **M**, pereopod 1; **N**, maxilliped article 3; **O**, pereopod 2; **P**, pereopod 4; **Q**, pereopod 7; **R**, uropod. Scale line represents 3.0 mm.

Description of female. Body about 2.8 times as long as wide, dorsum smoothly vaulted, coxae visible in dorsal view. Eyes about 0.5 width of cephalon. Pleonite 1 longest, pleonites 2–5 about equal in length; pleonites 1–4 becoming progressively narrower towards posterior. Lateral margins of pleonites 1–3 bent laterally; posterolateral margins of pleonite 5 acute. Pleotelson lateral margins weakly turned up, converging smoothly to rounded apex.

Antennule extending to posterior of eyes; article 3 anterodistal angle not produced. Antenna with 10 articles, extending to pereonite 2.

Mandible palp article 2 with distomedial margin lobate; article 3 with about 9 setae. Maxillule with 4 terminal spines. Maxilla with 2 spines each on medial and lateral lobe respectively. Maxilliped article 3 with 3 terminal spines.

Pereopod 1 dactylus with prominent nodule on anterior margin, weak nodule on posterior margin. Pereopods 2–4 with dactylus nodules progressively increasing in prominence; posterior margin of dactylus with 2 nodules. Pereopod 6 with 3 spines on propodus, merus with single spine at posterodistal angle. Pereopod 7 propodus with 3 spines on palm, scattered small spine on medial margin.

Pleopods 3–5 with prominent, highly folded proximomedial lobe on endopod; peduncle lateral margin with prominent lobe. Endopods of pleopods 3 and 4 each with 3 weakly developed lobes, endopod of pleopod 5 with 3 large folded lobes. Uropod with rami rounded, subequal in length, extending clearly beyond posterior of pleotelson.

Colour. Pale tan with abundant brown chromatophores.

Size. Females 14.0–16.0 mm.

Remarks. This species is readily identified by the smoothly rounded pleotelson, uropods extending beyond the posterior margin of the pleotelson, pleonite 1 being longest, ventrolateral margins of pleonites 1–3 being bent upwards, and antennule article 3 not being produced.

The most similar species is *Anilocra dimidiata,* but *A. soelae* differs from that species in having a shorter

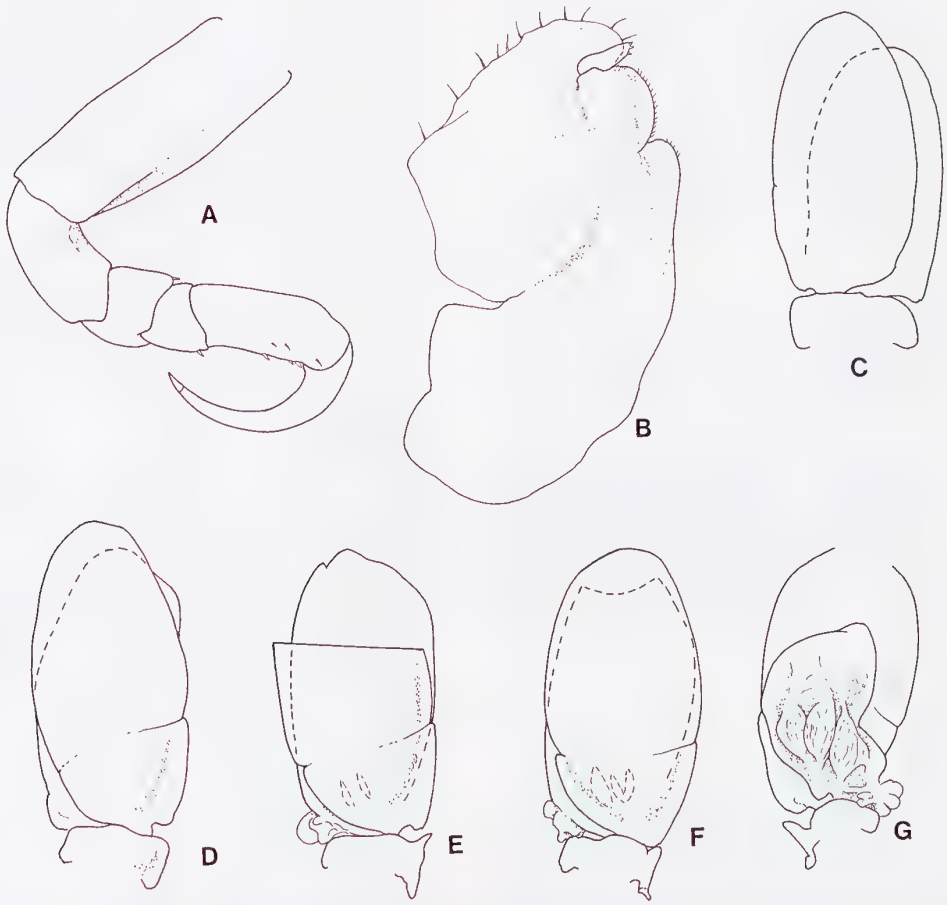

Fig. 19. *Anilocra soelae* n. sp., female 15.5 mm (NTM Cr4244). **A,** pereopod 6; **B,** maxilliped; **C,** right pleopod 1; **D–F,** left pleopods 2 to 4 respectively; **G,** left pleopod 5, posterior view.

antennule, more prominent pereopod nodules, an evenly rounded pleotelson, posterolateral margin of pleonite 5 not strongly produced and a shorter uropod exopod.

Host. Not known.

Distribution. North West Shelf, Western Australia.

Etymology. Named after the research vessel FRV *Soela.*

Anilocra koolanae n. sp.

Figs 20, 21

Material examined. HOLOTYPE: female, (ovig 29.0), off Koolan Island, WA, 8 Aug 1970, coll. F.C. van Ingen (WAM 598-85).

Type locality. Koolan Island, Yampi Sound, Northern WA, 16°08′S 123°45′E.

Description. Body about 3.0 times as long as wide. Eyes small, about 0.3 width of cephalon. Pereonite 7 less than half as long as pereonite 6. Pleonite 1 not visible in dorsal view. Pleonites with lateral margins strongly produced ventrally, concealing pleopod peduncles in lateral view. Pleotelson about twice as long as wide, more than twice as long as pleon; lateral margins convex, converging to narrowly rounded caudomedial lobe; lateral margins not upturned; medial longitudinal ridge strongly developed.

Antennule extending to posterior of eye, article 3 anterodistal margin weakly produced. Antenna with 10 articles, extending to posterior of pereonite 2.

Mandible palp broad, article 2 distolateral margin produced to form lobe; article 3 bent laterally with 11 setae along distomedial margin. Maxilliped article 3 with 3 terminal spines.

Pereopods all robust; pereopods 1–4 with nodule on anterior margin of dactylus. Pereopod 7 with 4 spines on posterolateral margin of propodus. Pereopods 5 and 6 with posterolateral margin of basis forming distinct keel.

Pleopod 1 exopod basally wide; lateral margin with obvious partial suture. Pleopod 2 similar to 1, but peduncle medial and lateral margins formed into lobes. Pleopods 3–5 endopods with prominent proximomedial lobe; exopods with distinct partial suture; pleopod 5 endopod with 3 large folds. Uropods extend clearly beyond pleotelson; endopod slightly longer than exopod; both rami narrowing gradually to pointed apex.

Male. Not known.

Size. Holotype, 29.0 mm.

Colour. Pale tan with sparsely scattered brown chromatophores.

Remarks. The long pleotelson with its narrowly produced apex, pereonite 7 less than half the length of pereonite 6, long narrow uropods, and the pleon with only 4 visible pleonites immediately differentiates this species from all others in the genus. The antennule has the anterodistal angle of article 3 produced, and the anterior margin of the dactylus of pereopods 1–4 have a nodule. These characters are also present in the *A. dimidiata* – *A. leptosoma* complex of species, but *A. koolani* is readily separated from those species by the characters listed above.

Host. Known only from the type locality.

Etymology. The name is taken from that of the type locality.

Anilocra apogonae n. sp.

Figs 22, 23

Anilocra sp.—Monod, 1976: 857, figs 8–12.

Material examined. HOLOTYPE: female (ovig 19.5), off Saint Helena Is., Moreton Bay, Qld, 24 Nov 1981, ex *Apogon fasciata,* coll. R.C. Willan (QM W12181).

PARATYPES: female (ovig 12.5), Coral Bay, Cobourg Peninsula, NT, 11°12.0′S 132°03.0′E, May 1983, ex *Apogon cooki,* coll. N.L. Bruce, (NTM Cr4245). Female (non-ovig 16.0), north side of Prince of Wales Is., Torres Strait, 2 July 1976, from tide pools, coll. D. Brown & W. Ponder (AM P36258). Lizard Island Group, Qld, Northern Great Barrier Reef, all ex *Cheilodipterus quinquelineatus:* female (imm 8.5), north-west Palfrey Is., 14 July 1985, 6 m (AM P36262); 2 females (ovig 12.0, non-ovig 11.5), north-west Palfrey Is., 15 July 1985, 6 m (AM P36260); 2 females (ovig 13.0, 11.5), lagoon entrance, 17 July 1985, 17 m (AM P36264, P36265); female (ovig 14.0), North Point Reef, Lizard Island, 18 July 1985, 12 m (AM P36259); female (ovig 11.5), Granite Bluffs, Lizard Island, 20 July 1985, 10 m (AM P36266); 3 females (ovig 16.0, non-ovig 12.5, 12.0), lagoon entrance patch reef, 21 July 1985, 10 m (AM P36263); female (non-ovig 11.0), eastern lagoon, 22 July 1985, 8 m (AM P36261), coll. N.L. Bruce, R. Springthorpe. 3 females (ovig 14.5, 13.5, non-ovig 11.0), male (9.5 mm), Bushy-Redbill Reef, 12°57′S 150°05′E, GBR, Qld, June 1975, no host (QM W10846). 2 males (12.5, 11.0), Magnetic Island, off Townsville, Qld, 14 July 1976, ex *Apogon cooki* (QM W10412). 2 females (ovig 16.3, 15.5), Lindeman Island, Cumberland Group, Qld, 1935, ex *Apogon cooki,* coll. G.P. Whitley (AM P11783). 2 females (ovig 15.0, non-ovig 13.0), same data as holotype (QM W10360). Female (ovig 19.0), Moreton Bay, Qld, Nov 1979, ex *Apogon fasciata,* coll. N. Svennivig (QM W10366).

Additional material. Two females, East Point Darwin, NT, 13 Sept 1982, coll. H.K. Larson (NTM Cr2299). 3 females, Darwin, NT, 12°58′S 132°10′E, 19 Oct 1981, 27 m, coll. H.K. Larson (NTM Cr2287, Cr2300). Aegathoid (7.5), north-east point, Fantome Island, Palm Group, Qld, 18 Apr 1986, on *Apogon cooki* coll. N.L. Bruce, R.T. Springthorpe (AM P36749). Female, South Percy Island, Qld, coll. Seargeant L. Lockwood (SAM C1729, examined by Hale, 1926). Female, Moreton Bay, Qld, 31 Mar 1975, ex "Goatfish"* (QM W10989). Female, off Saint Helena Island, Moreton Bay, Qld, 2 Sept 1979, 6 m (QM W11012). 3 females, Moreton Bay, Qld, no date, apogonid hosts. (QM W10418).

Type locality. Off Saint Helena Island, Moreton Bay, south-eastern Queensland, ca. 27°23′S 153°14′E.

Description of female. Body about 2.5 times as long as wide, dorsum strongly vaulted; lateral margins of pereonites 4–6 thickened. Pleonite 1 about twice as long as pereonite 2; pleonites 2–5 subequal in length; dorsal posterolateral margin of pleonites 4 and 5 strongly produced, acute. Pleotelson about 1.5 times as long as wide, lateral margins strongly bent dorsally; posterior

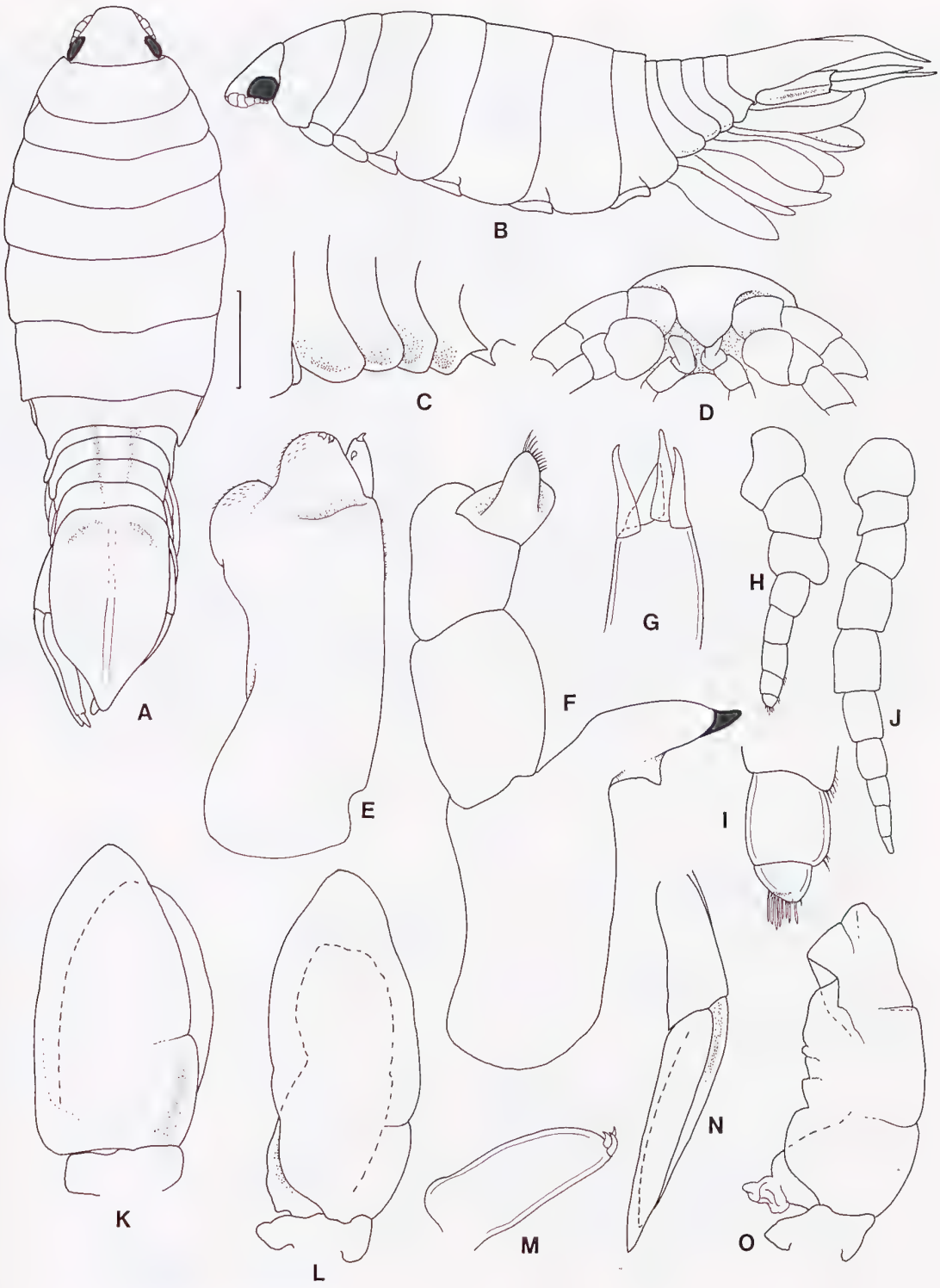

Fig. 20. *Anilocra koolanae* n. sp., holotype. **A**, dorsal view; **B**, lateral view; **C**, pleonites, lateral view; **D**, frons; **E**, maxilla; **F**, mandible; **G**, maxillule apex; **H**, antennule; **I**, antennule apex; **J**, antenna; **K**, pleopod 1; **L**, pleopod 2; **M**, maxilliped article 3; **N**, uropod; **O**, pleopod 3. Scale line represents 4.0 mm.

margin laterally indented, then forming broadly rounded lobe.

Antennule extending to posterior of eye; anterodistal margin of article 3 not produced. Antenna extending to posterior of pereonite 1, composed of 8 articles; article 5 with 3 feebly plumose setae at posterodistal angle.

Mandible palp article 2 lateral margin extended, forming lobe; terminal article with apex subtruncate, lateral margin weakly folded. Maxilla with 2 spines each on medial and lateral lobe respectively. Maxilliped article 3 with 3 spines.

Pereopod 1 dactylus without nodules; pereopods 2–4 with prominent nodule on dactylus anterior margin, less prominent nodule on dactylus posterior margin; dactylus progressively increasing in length from pereopod 1–4. Pereopod 6 carpus with 1 spine at posterodistal angle; propodus 4 spines on posterior margin and 2 small submarginal spines. Pereopod 7 propodus with 4 spines on posterior margin and 3 submarginal spines.

Pleopods 3–5 proximomedial lobe large, convoluted. Pleopod 3 endopod without folds, pleopod 4 endopod with weak folds, pleopod 5 endopod with 3 simple folds. Uropod rami extending beyond posterior of pleotelson; exopod about two thirds width of, and slightly larger than endopod, curving medially; endopod straight, distal margin broadly rounded, both margins convex.

Male. Maxilliped article 3 with 4 spines; maxillule with 4 terminal spines. Pleopods similar to female, but pleopod 2 with appendix masculina, and reduced folding on endopods of pleopods 3–5. Uropod exopod proportionally longer than in female. Pereopods 2–4 with nodule only on anterior margin of dactylus.

Colour. All specimens densely covered by brown chromatophores; ground colour pale yellow.

Size. Ovigerous females: 11.5–19.5 mm; non-ovigerous females: 11.0–16.0 mm; males 9.5–12.5 mm.

Variation. Body width varies from 2.5–2.8 times as long as wide. Nodules on anterior margin of the dactylus of pereopods 2–4 may vary in size, but are always conspicuously large.

Remarks. Commonly encountered on apogonid hosts, *A. apogonae* is easily recognised by the thickened margins of pereonites 5–7, absence of dactylus nodules on pereopod 1 and their prominence on pereopods 2–4, pleonite 1 being twice as long as 2, acute posterolateral angles to pleonites 4 and 5, and the strongly upturned pleotelson lateral margins.

The figures of *Anilocra* sp. from an apogonid host given by Monod (1976) agree entirely with the present material.

Hosts. *Apogon cooki, A. fasciatus* and *Cheilodipeturus quinquelineatus;* sight record on *Apogon cyanosoma*, Palm Group. At Lizard Island there was only ever one isopod per host, always situated in a dorsal position above the eyes. Monod (1976) recorded *Apogon kallopterus.*

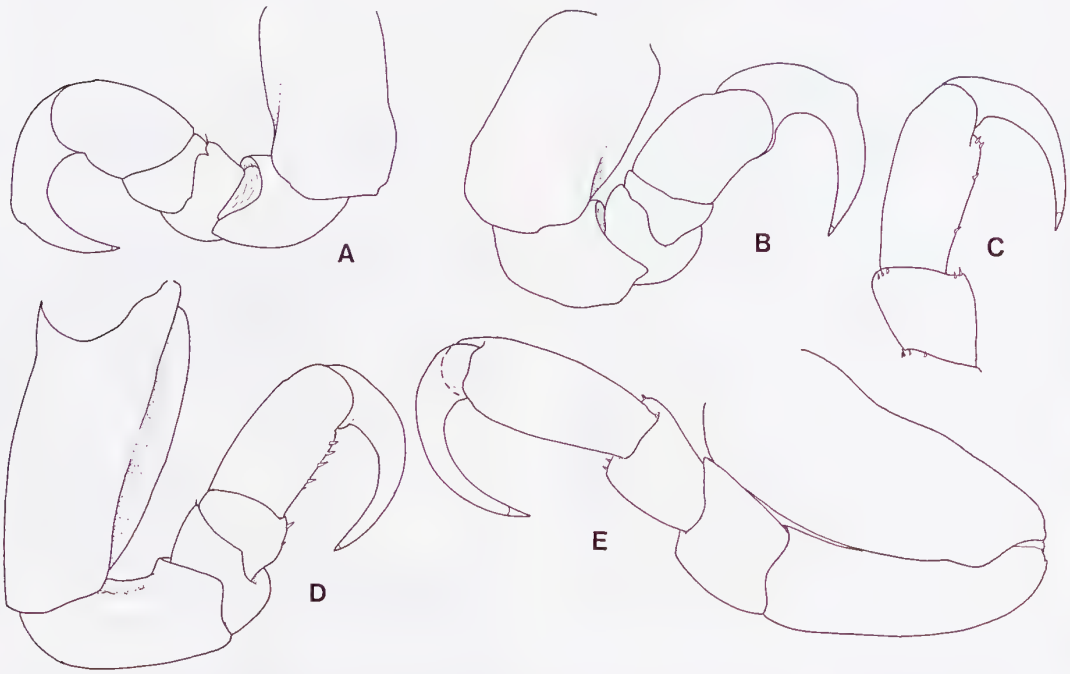

Fig. 21. *Anilocra koolanae* n. sp., holotype. **A**, pereopod 1; **B**, pereopod 2; **C**, pereopod 7, medial view of distal articles; **D**, pereopod 6; **E**, pereopod 17.

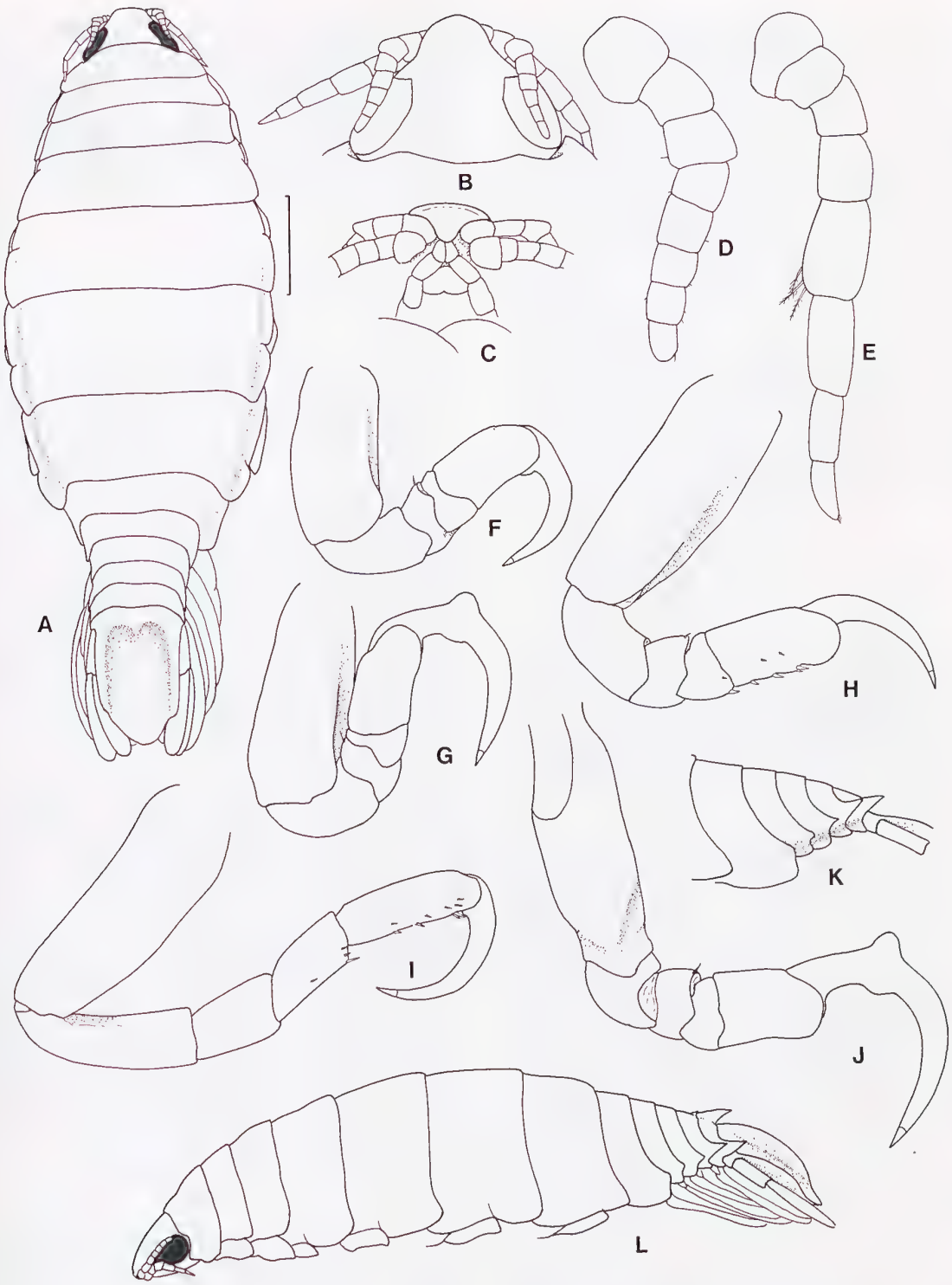

Fig. 22. *Anilocra apogonae* n. sp., A–C, K, L, holotype, remainder female 15.0 mm (QM W10360). **A,** dorsal view; **B,** cephalon; **C,** frons; **D,** antennule; **E,** antenna; **F,** pereopod 1; **G,** pereopod 2; **H,** pereopod 6; **I,** pereopod 7; **J,** pereopod 4; **K,** pleon, lateral view; **L,** lateral views. Scale line represents 3.0 mm.

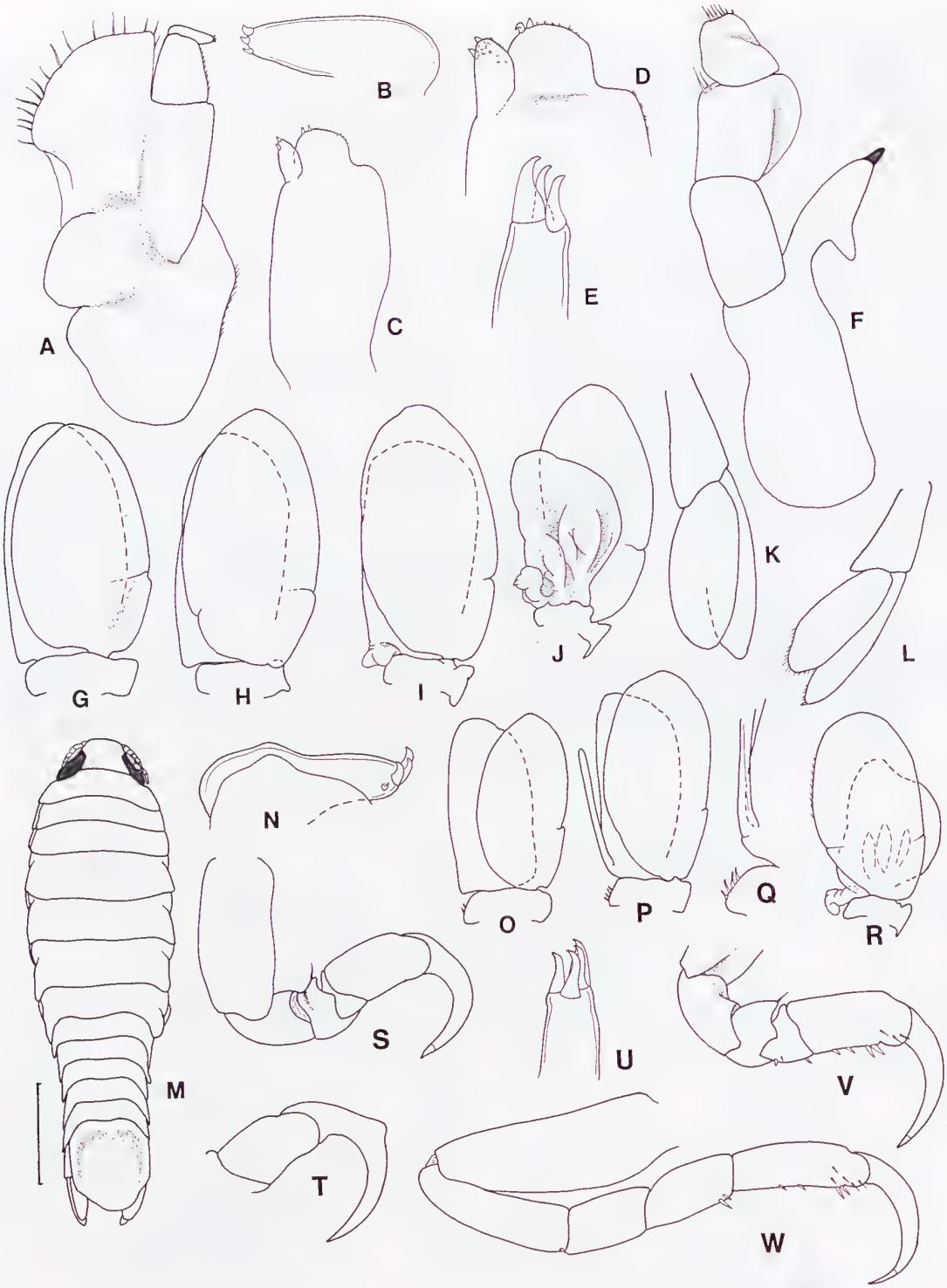

Fig. 23. *Anilocra apogonae* n. sp., A–K, female 15.5 mm (QM W10360); L–W, male 9.5 mm (QM W10846). **A**, maxilliped; **B**, maxilliped article 3; **C**, maxilla; **D**, maxilla apex; **E**, maxillule apex; **F**, mandible; **G–J**, pleopods 1 to 3, 5 respectively; **K**, uropod; **L**, uropod; **M**, dorsal view; **N**, maxilliped apex; **O**, pleopod 1; **P**, pleopod 2; **Q**, pleopod 2, medial margin detail; **R**, pleopod 5; **S**, pereopod 1; **T**, pereopod 2, propodus dactylus; **U**, maxillule apex; **V**, pereopod 6, distal articles; **W**, pereopod 7. Scale line represents 2.0 mm.

Distribution. On the mainland coast and continental islands, but not recorded from outer reefs. Cobourg Peninsula and Darwin, Northern Territory. Torres Strait, Lizard Island, Palm Group, Magnetic Island, Townsville, Lindeman Island, South Percy Island and Moreton Bay, Queensland. Also Ambon, Indonesia (Monod, 1976).

Etymology. The name is derived from that of the type host genus.

Anilocra longicauda Schiödte & Meinert
Figs 24, 25

Anilocra longicauda Schiödte & Meinert, 1881: 113, pl. 8 figs 7, 8.—Monod, 1934: 12, pls 20, 21, 25A-C; Trilles, 1975a: 308, pl. 1 figs 4, 5.
Anilocra dimidiata.—Richardson, 1910: 18 (part).
Unconfirmed: Gerstaecker, 1882: 261; Nierstrasz, 1915: 83; 1931: 129; Serène, 1937: 69.

Material examined. LECTOTYPE: female (ovig 35.0), Singapore, 9 Mar 1872, udvendig paa Hardit af Fisk, coll. H. Koch (ZMC). PARALECTOTYPE: female (ovig 27.0), Poulo Condor (Cochin chine), R. Germain, 446-68, label No. 43 (male missing) (MNHN Is. 504).

Non-type: female (ovig 41.0), north of Port Hedland, WA, 18/19 Apr 1983, depth 80 m, coll. R. Williams (NTM Cr2292). Female (ovig 39.0), Marion Reefs, Qld, ca. 19°15′S 152°13′E, 23 Aug 1977, ex *Priacanthus* sp., depth 8 m, coll. N. Coleman (AM P36286). 2 females (ovig 51.0, non-ovig 32.0), Swains Reefs, Qld, ca. 22°4′S 152°30′E, 6 June 1967, ex *Plectorhynchus goldmani,* coll. B. Goldman (AM P36267).

Additional material. Female (head missing), North West Shelf, WA, 19°5.5′S 118°25.5′E, 2 June 1985, coll. B.C. Russell (NTM Cr4246). 2 females, North West Shelf, WA, 19°08.6′S 118°03.5′E, 16 April 1983, depth 82–84 m, on *Plectorhynchus pictus,* coll. P. Blyth on FRV *Soela* (NTM Cr2311). 2 females, Krakatua Island, Indonesia, 6°06′S 105°26′E, 15 Sept 1984, no host. La Trobe University 1984 Krakatua Expedition (NMV J12952, one at Museo Zoologicum, Bogor, Indonesia). 2 females (USNM 40997, 40999), Philippines, examined by Richardson (1910).

Types. Schiödte & Meinert (1881) examined 5 specimens, listing 3 from Singapore and 2 from Poulo Condor. Only two type specimens were located and the specimen from Singapore is designated as lectotype. The type specimens examined here do not agree with Schiödte & Meinert's lengths for ovigerous females (41–43.5 mm) but rather to the length for non-ovigerous females (31–37.5 mm).

Type locality. Singapore, 1°15′N 103°50′E, the locality of the lectotype.

Description of female. Body about 3.5 times as long as wide, dorsal surface strongly vaulted; coxae scarcely visible in dorsal view. Rostrum anterior margin weakly indented in dorsal view. Eyes occupying about 0.4 width of cephalon. Pleon about 0.6 width of pereon. Pleonite 1 largely concealed by pereonite 7; posterolateral margins of pleonites 1–3 rounded; dorsal posterolateral margins of pleonite 5 acute, weakly produced. Pleotelson flat, lateral margins not upturned; lateral margins curving to form subacute apex.

Antennule extending to posterior of cephalon. Antenna with 10 articles, extending half way along pereonite 1.

Mandible palp article 2 distomedial margin produced to form lobe; article 3 medial margin folded, lateral margin with 14 setae. Maxillule with 4 terminal spines. Maxilla with 2 spines, each on medial and lateral lobes respectively. Maxilliped article 2 with 2 terminal spines.

Pereopods 1–4 short, dactylus robust, abruptly curved, without nodules. Pereopods 5–7 with dactylus smoothly curved.

Pleopods prominent in dorsal view. Pleopod 1 with 4 coupling hooks on peduncle medial margin. Pleopods 3 and 4 each with folded endopod; pleopod 5 endopod with massive and complex folding. Pleopods 3–5 endopods with prominent proximomedial lobe, peduncle lateral margin with small proximal appendiculate lobe. Uropods not extending beyond pleotelson, exopod slightly shorter than endopod, both rami bluntly rounded.

Male. None examined.

Colour. Very dark brown, appearing black.

Size. Females 27.0–31.0 mm.

Variation. The type material and the smaller Australian specimens (NTM Cr2311, 23.0 and 30.0 mm) have the pleotelson more broadly rounded than the large specimens from *Priacanthus* and *Plectorhynchus.* The non-ovigerous female (AM P36286) had 3 spines on maxilliped article 3, 3 spines on the maxillule and more spines on pereopod 7.

Remarks. This large species is easily recognised by the short and abruptly recurved anterior pereopod dactyls which totally lack nodules, short antenna, pleonite 1 being largely concealed by pereonite 7, and the long and flat pleotelson.

Monod (1934) included *Anilocra cavicauda* Richardson in the synonymy for *A. longicauda,* this later being followed by Trilles (1975). Examination of the type of *A. cavicauda,* shows it to be abundantly distinct from *A. longicauda* with nodulose pereopods, straight sided and upturned pleotelson lateral margins, and slender uropods extending beyond the pleotelson. Suplementary notes and figures for *A. cavicauda* are given elsewhere in this work.

Hosts. *Plectorhynchus goldmani, Diagramma picta* and *Priacanthus* sp.; sight record on caudal peduncle of *D. picta* at Lizard Island.

Distribution. Swains Reefs, Great Barrier Reef, Marion Reef, Australian Coral Sea; North West Shelf of Western Australia; Krakatua, Indonesia; previous records from Singapore (Schiödte & Meinert, 1881), Annan (Monod, 1934) and Poulo Condor, Vietnam (Schiödte & Meinert, 1881); Philippines (Richardson, 1910, as *A. dimidiata).*

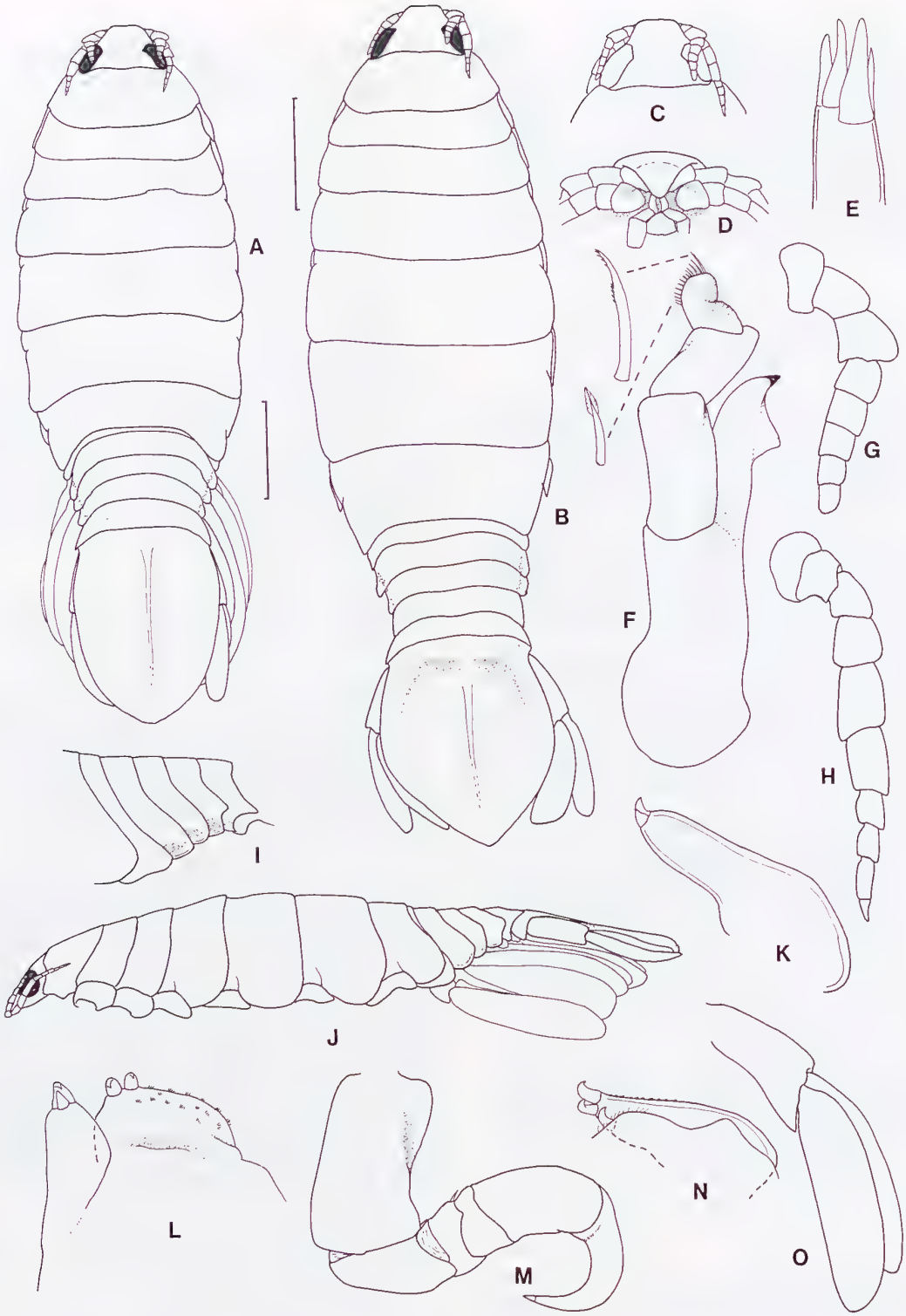

Fig. 24. *Anilocra longicauda,* A, J, lectotype; N, female 32.0 mm, Swains (AM P36267); remainder female 39.0 mm, ex *Priacanthus* (AM P36286). **A,** dorsal view; **B,** dorsal view; **C,** cephalon; **D,** frons; **E,** maxillule apex; **F,** mandible; **G,** antennule; **H,** antenna; **I,** pleon, lateral view; **J,** lateral view; **K,** maxilliped article 3; **L,** maxilla apex; **M,** pereopod 1; **N,** maxilliped article 3; **O,** uropod. Scale lines represent 5.0 mm.

Anilocra ankistra n. sp.

Figs 26, 27, 28

Material examined. All material from North West Shelf, WA.

HOLOTYPE: female (ovig 43.5), north-west of Beagle Bay, 15°10.4′S 121°04.7′E, 11 Feb 1984, depth 449 m, Engel trawl over muddy bottom, coll. FRV *Soela* (WAM 608-85).

PARATYPES: female (ovig 36.0), 127 nautical miles north-west of Port Hedland, 18°26′S 117°36′E, 11 April 1982, depth 418 m, coll. L.M. Marsh on FRV *Soela* (WAM 603-85). Female (ovig 20.0), 17°59.0′S 118°19.9′E, 27 Feb 1984, depth 418 m, coll. A.J. Bruce on FRV *Soela* (NTM Cr636). Female (non-ovig 23.0), 17°30.1′S 118°28.9′E, Feb 1984, trawled, 504–506 m, coll. A.J. Bruce (NMT Cr639). Male?, (18.0), 19°25.2′S 119°11.8′E, 4 Feb 1984, trawled 356 m, coll. A.J. Bruce on FRV *Soela* (NTM Cr640). Female (non-ovig 21.0), 17°16.3′S 119°01.5′E, 3 Feb 1984, trawled 458 m, coll. A.J.

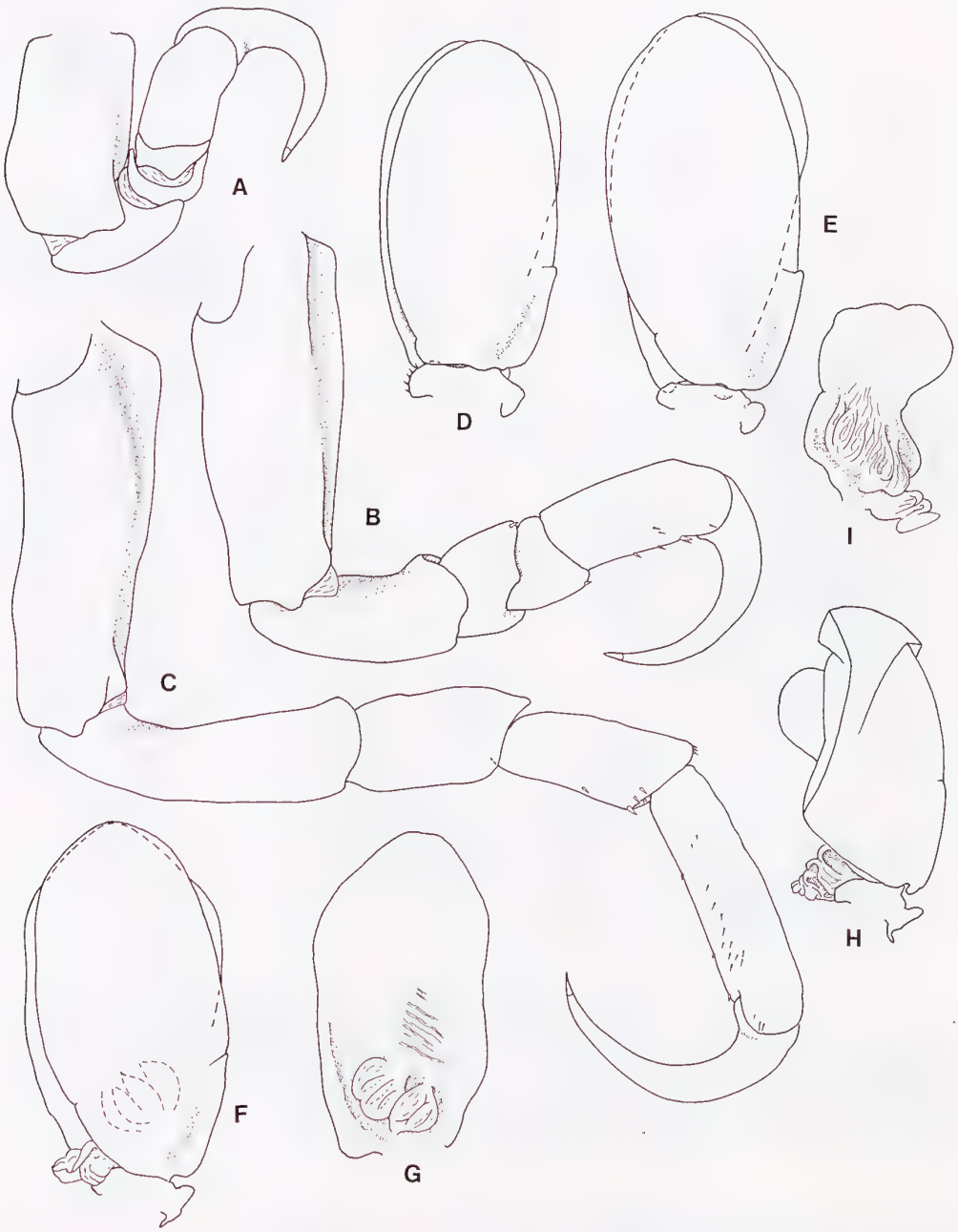

Fig. 25. *Anilocra longicauda,* female 39.0 mm ex *Priacanthus (AM P36286).* **A,** pereopod 2; **B,** pereopod 6; **C,** pereopod 7; **D–F,** pleopods 1 to 3 respectively; **G,** pleopod 3 endopod, posterior view; **H,** pleopod 5; **I,** pleopod 5, posterior view.

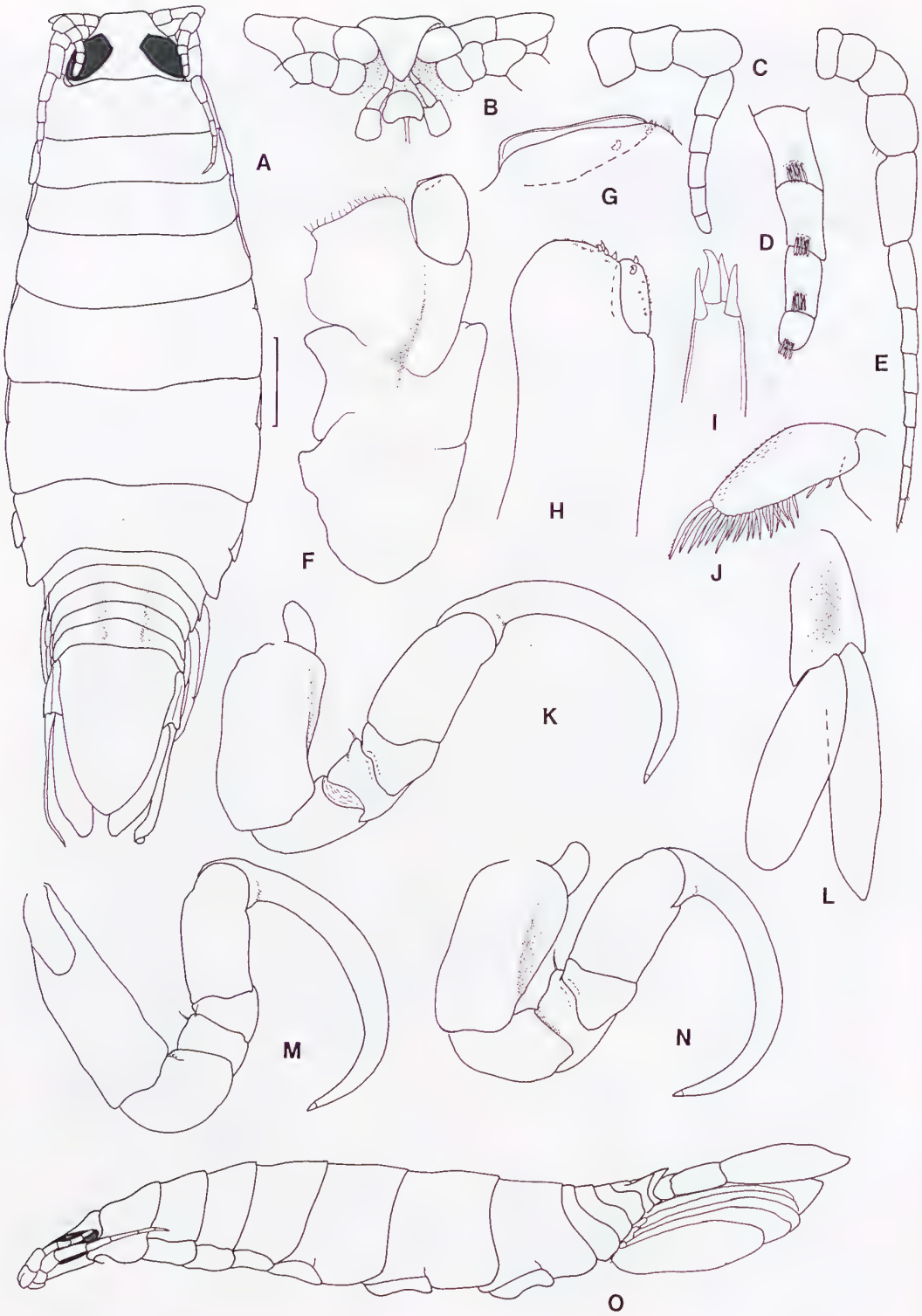

Fig. 26. *Anilocra ankistra* n. sp., A, B, O, holotype, remainder female 36.0 mm (WAM 603-85). **A**, dorsal view; **B**, frons; **C**, antennule; **D**, antennule, ventral surface of articles 5 to 8; **E**, antenna; **F**, maxilliped; **G**, maxilliped article 3; **H**, maxilla; **I**, maxillule apex; **J**, mandible palp article 3; **K**, pereopod 1; **L**, uropod; **M**, pereopod 4; **N**, pereopod 2; **O**, lateral view. Scale line represents 5.0 mm.

Bruce on FRV *Soela,* (NTM Cr642). Female (non-ovig 22.0), 18°41.6′S 117°18.6E, 25 Apr 1983, trawled 360–320 m (NTM Cr4247). Female (non-ovig 31.0), 18°06.5′S 117°45′E, 7th Apr 1982, depth 472–520 m, coll. M. McGrouther & J. Paxton on FRV *Soela,* (AM P36269).

Type locality. North West Shelf of Western Australia, 15°10.4′S 121°04.7′E.

Description of female. Body slightly more than 3 times as long as wide; dorsum only moderately vaulted. Coxae 2–4 broad, subrectangular, coxae 5–7 posteriorly rounded. Cephalon dorsal surface flat; rostrum prominent, anterior margin slightly indented. Eyes about 0.7 width of cephalon, facets distinct. Pleonites all visible; lateral margins not produced; dorsal posterolateral angles of pleonites 4 and 5 weakly produced, acute. Pleotelson flat, lateral margins not

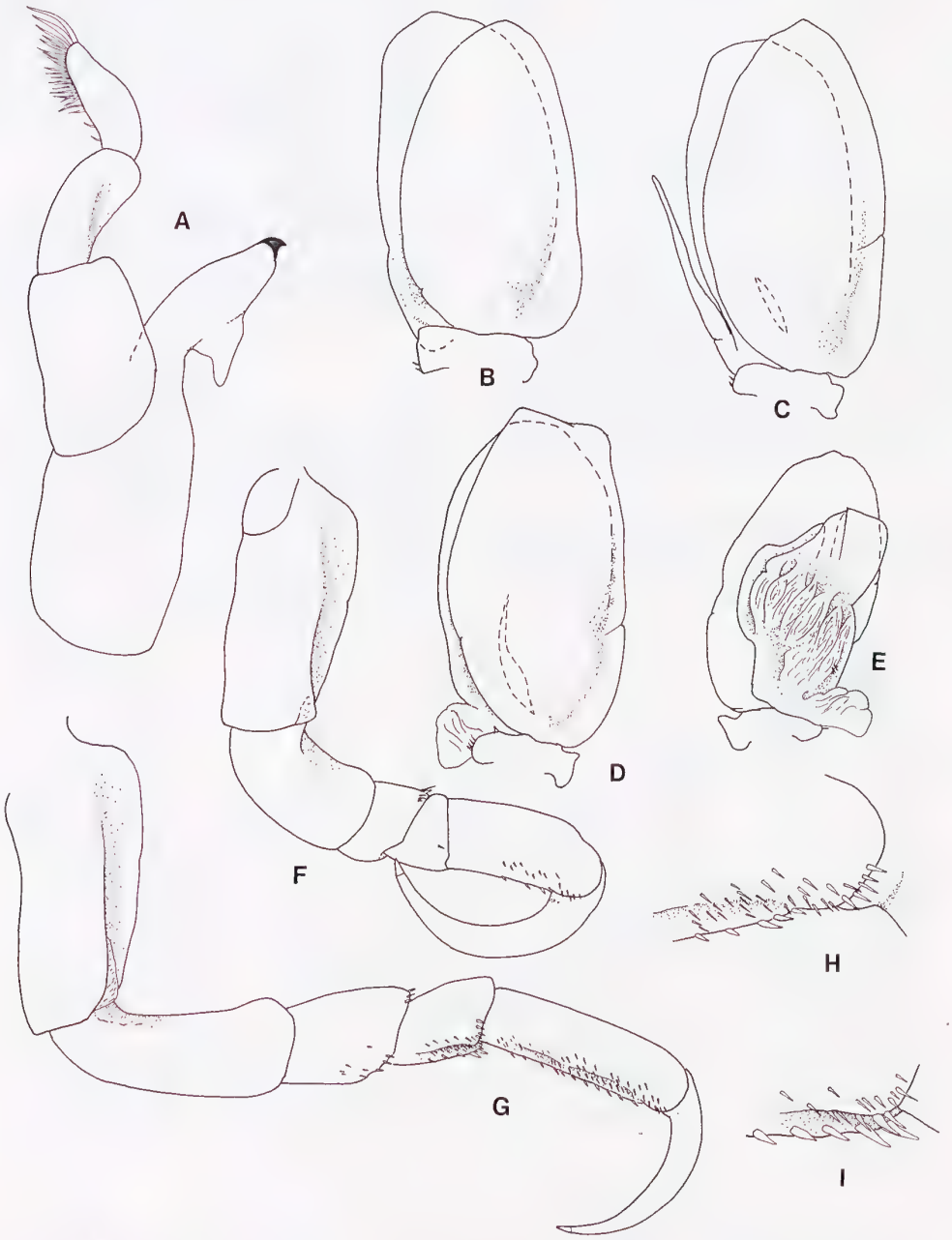

Fig. 27. *Anilocra ankistra* n. sp., female 36.0 mm (WAM 603-85). **A,** mandible; **B–D,** pleopods 1 to 3 respectively; **E,** pleopod 5, posterior view; **F,** pereopod 6; **G,** pereopod 7; **H,** pereopod 7 propodal palm, detail; **I,** pereopod 7 merus, detail.

upturned, converging smoothly to caudomedial point.

Antennule extending to posterior of cephalon; anterodistal angle of article 3 produced. Antenna composed of 12 articles, extending to pereonite 3; articles 6–12 elongate.

Mandible incisor recurved; palp article 3 elongate, lateral margin with 25 stout setae, distal setae longest. Maxillule with 4 terminal spines. Maxilla lateral lobe with 4 spines, medial 2. Maxilliped article 3 small, largely concealed in ventral view by article 2; provided with 3 recurved spines.

Pereopods 1–4 with dactylus about twice as long as propodus; pereopods 5–7 with dactylus progressively decreasing in length. Pereopod 1 basis slightly longer than propodus, basis of pereopods 2–7 becoming progressively longer towards posterior. Pereopod 7 carpus and propodus medial margins with abundant small spines.

Pleopod 1 with peduncle about twice as wide as long, peduncles of pleopods 2–5 about 3 times wider than long. Pleopod 2 with appendix masculina retained. Pleopods 3–5 endopods with large and convoluted proximomedial lobe; pleopods 2–4 endopod with single simple fold; endopod of pleopod 5 massively and complexly folded. Uropod rami extending clearly beyond posterior of pleotelson, exopod slightly longer than endopod, apex acute; endopod apex broadly rounded.

Male. Body about 3.2 times as long as wide; appendages similar to those of female, but pleopod 2 appendix masculina proportionally longer. As the female of this species retains the appendix masculina, it was not possible to positively identify males.

Colour. Densely covered by chromatophores which give a dark brown appearance, extending onto ventral surface of cephalon and appendages including the ventral surface of pleopod 1.

Size. Ovigerous females: 20.0–43.5 mm; non-ovigerous: 21.0–31.0 mm; and male at 18.0 mm.

Remarks. This species is easily distinguished from all others by the large eyes, very long dactylus on the anterior pereopods, and generally weakly vaulted body shape. The elongate third mandible palp article, presence of 4 spines on the maxilla lateral lobe, and retention of the appendix masculina in the female are unique characters within the genus.

Hosts. Not known.

Distribution. Trawled from several localities on the North West Shelf of Western Australia.

Etymology. The name derives from the Greek for fishhook, *ankistron,* and aludes to the long dactyli.

Anilocra morsicata n. sp.

Figs 29, 30

Material examined. HOLOTYPE: female (23.5), off Fraser Island, south-eastern Qld, 23°28′S 153°19′E, 20 Sept 1980, depth 562 m, coll. Q.F.S. (QM W10186).

Type locality. Off south-eastern Queensland, 23°28′S 153°19′E.

Description. Body 3 times as long as wide, lateral

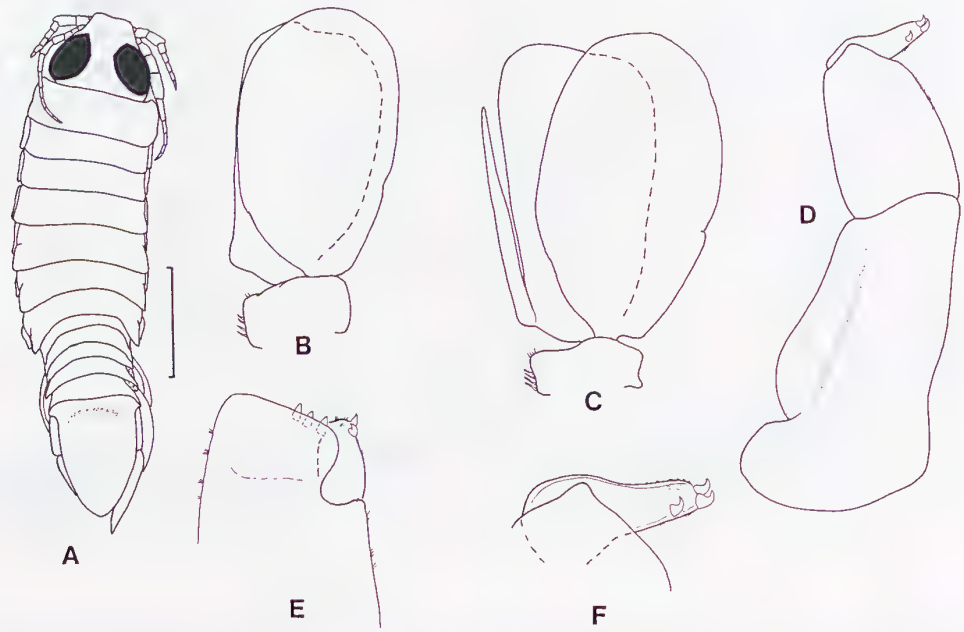

Fig. 28. *Anilocra ankistra* n. sp., ?male 18.0 mm (NTM Cr 649). **A**, dorsal view; **B**, pleopod 1; **C**, pleopod 2; **D**, maxilliped; **E**, maxilla apex; **F**, maxilliped article 3. Scale line represents 4.0 mm.

margins subparallel in dorsal view; dorsum strongly vaulted. Cephalon anterior margin wide, rostrum scarcely developed in dorsal view; eyes about 0.40 width of cephalon. Medial posterior margin of pereonites 3–7 weakly produced. Lateral margins of pleonites not posteriorly produced, not acute; posterodorsal margin of pleonites 3–5 weakly produced. Pleotelson lateral margins not turned up, posterior margin evenly rounded; anterodorsal surface with depression.

Antennule extending to posterior of eye; article 3 not produced. Antenna with 12–14 articles, extending to pereonite 3; article 4 with plumose setae along posterior margin; articles 7–11 posterodistal margin weakly lobed.

Mandible palp article 3 not folded, distolateral margin with 10 setae; article 2 distolateral margin with 2 setae. Maxillule with 4 terminal spines. Maxilla with 2 spines

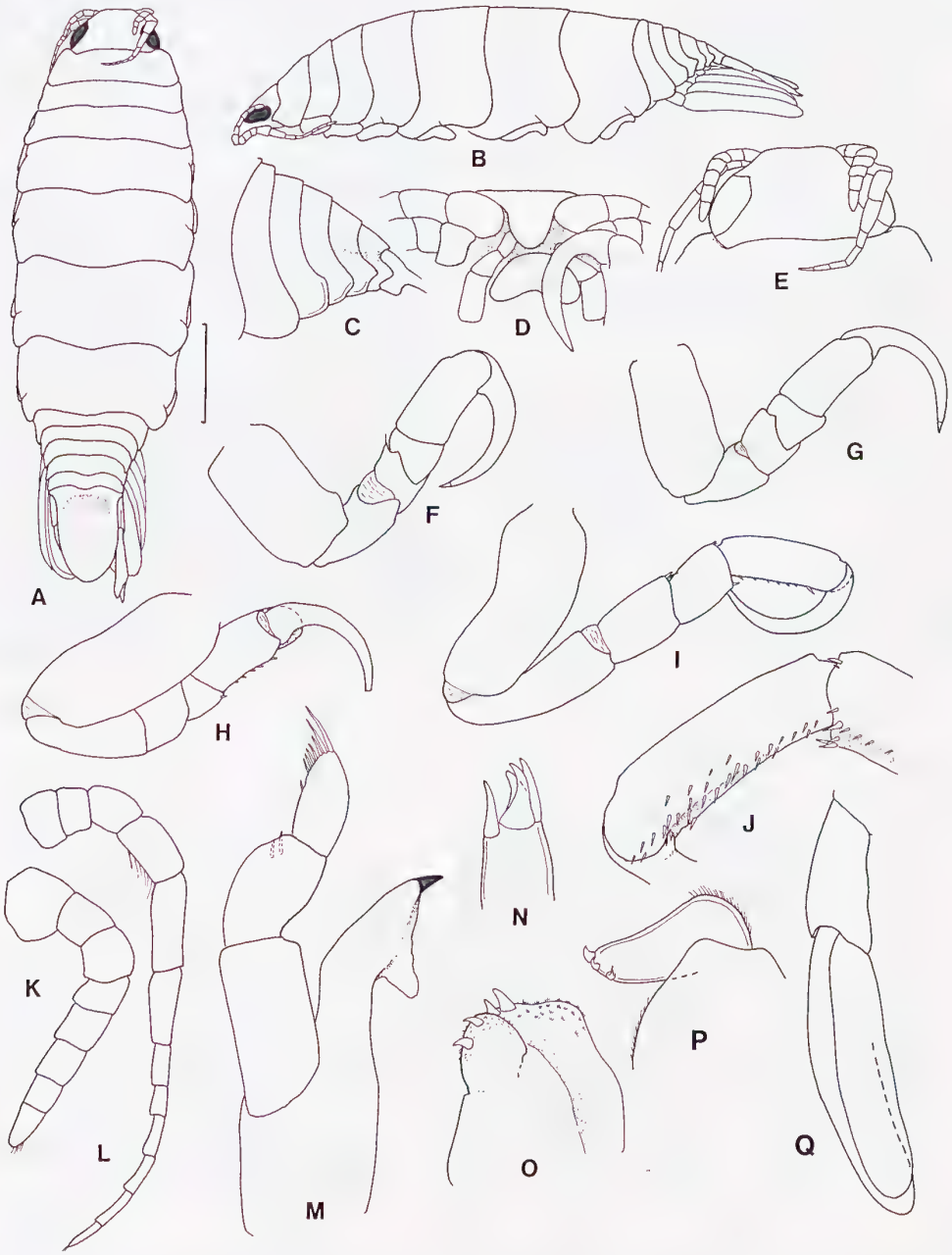

Fig. 29. *Anilocra morsicata* n. sp., holotype. **A,** dorsal view; **B,** lateral view; **C,** pleon, lateral view; **D,** frons; **E,** cephalon; **F,** pereopod 1; **G,** pereopod 2; **H,** pereopod 6; **I,** pereopod 7; **J,** pereopod 7, merus, propodus, lateral view; **K,** antennule; **L,** antenna; **M,** mandible; **N,** maxillule apex; **O,** maxilla apex; **P,** maxilliped article 3; **Q,** uropod. Scale line represents 4.0 mm.

each on medial and lateral lobes respectively. Maxilliped article 3 with 3 recurved spines.

Pereopods 1–4 dactylus without nodules, smoothly and shallowly curved; pereopods 2 and 3 similar to pereopod 1. Pereopod 7 with abundant spines on posteromedial margin to carpus and propodus. Pereopod 6 similar to 7 but articles shorter, especially merus and carpus.

Pleopod 1 rami margin converging to narrowly rounded apex. Pleopod 2 similar to 1, but vestigial appendix masculina present on endopod. Pleopod 3 with endopod shorter and more bluntly rounded than exopod, without folds. Pleopod 4 same as 3. Pleopod 5 endopod with 3 folds; peduncles of pleopods 1–5 with 4 coupling hooks. Uropods extending beyond pleotelson, exopod slightly longer than endopod; apex of endopod bluntly rounded.

Male. Not known.

Colour. Dorsal surfaces of pereon and pleon dark brown; antennule, antenna, pereopods (except basis), pleopods and uropods almost entirely unpigmented.

Size. Holotype, 23.5 mm.

Remarks. This species is most similar to *Anilocra meridionalis* Richardson (see Brusca, 1981). The differences are that *A. morsicata* has less strongly curved dactyls, more narrowly rounded rami on pleopods 1 and 2, longer and more narrowly rounded uropod rami and, most obviously, has a very short, bluntly rounded rostrum.

Hosts. Not known.

Distribution. Known only from the type locality.

Etymology. The name is derived from the Latin, *morsicatus,* to bite continually.

Anilocra pomacentri n. sp.

Figs 31, 32

Material examined. All Great Barrier Reef, Qld. HOLOTYPE: female (ovig 12.5), Wistari Reef, Capricorn Group, 25 March 1985, from *Chromis nitidus,* coll. R. Adlard (QM W12182).

PARATYPES: 2 females (11.0, non-ovig 8.0, imm 7.0), male? (6.5), same data as holotype (QM W12183). Female (non-ovig 9.5, imm 6.0), same locality and host, 3 Mar 1985, coll. R. Adlard (QM W12184). Female (ovig 10.5), male (9.8), sex indeterminate (7.5), Lizard Island, Qld, back reef, 22 Mar 1985, ex *Pomacentrus melanochir,* 10 m, coll. R. Pitcher (AM P36270). Female (non-ovig 11.5), reef pass, north end of Carter Reef, north-east of Lizard Island, 11 Feb 1986, on *Chromis atripes,* 18 m, coll. N.L. Bruce & N. Preston (AM P36285).

Additional material. Female, Waining Reef, north-east of Lizard Island, 14°30′S 145°15′E, 4 May 1985, on *Pomacentrus amboinensis,* coll. R. Pitcher (AM P36751). 3 females, Myrmidon Reef, north-east of Townsville, 18°16′S 147°27′E, 20 Feb 1986, on *Chromis margaritifer,* coll. P. Doherty (AM P36758). Palm Group, Qld series:- from *Pomacentrus melanopterus:* 2 females (ovig 15.0, 13.8), male (5.5), north-eastern point, Fantôme Island, 18 April 1986, 7 m (AM P36757); from *Pomacentrus lepidogenys:* 3 females (ovig 10.2, non-ovig 6.0, 5.5), north bay, Pelorus Island, 9 April 1986, 9 m (AM P36756); 3 females (ovig 12.5, 10.5, 10.0), north-eastern reef, Orpheus Island, 15 April 1986, 8 m (AM P36753); 2 females (ovig 15.0,11.5), north-eastern reef, Orpheus Island, 16 April 1986, 10 m (AM P36752); from *Pomacentrus moluccensis:* 2 females (non-ovig 6.0, 6.5), north bay, Pelorus Island, 9 April 1986, 9 m (AM P36755); female (ovig 9.1), north-eastern reef, Orpheus Island, 20 April 1986, 7 m (AM P36754); also 11 uncatalogued males and juveniles from *P. melanopterus* (1), *P. lepidogenys* (2), and *P. moluccensis* (8); all coll. N.L. Bruce, R.T. Springthorpe.

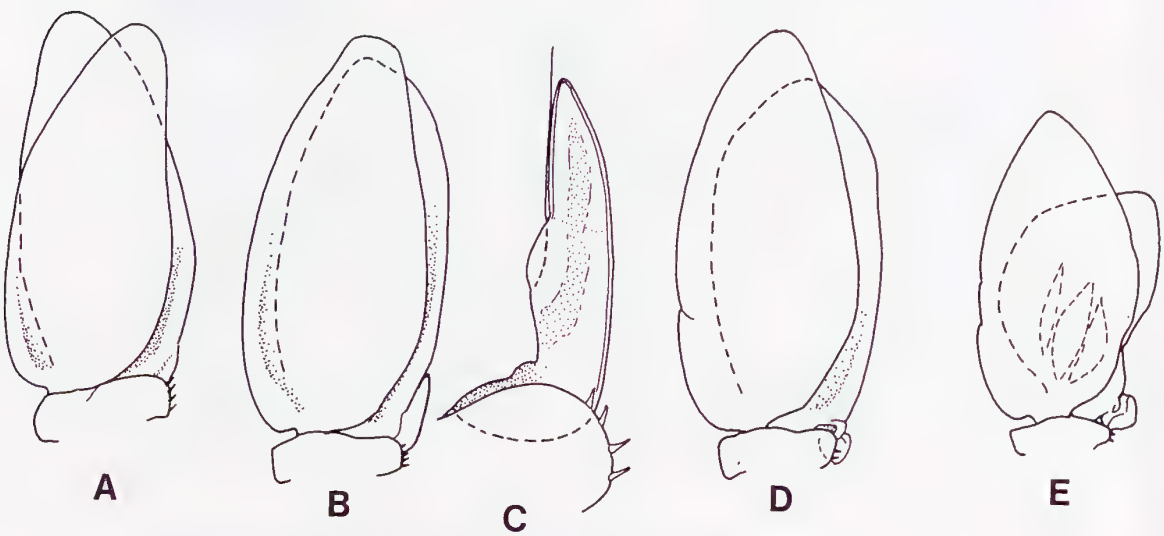

Fig. 30. *Anilocra morsicata* n. sp., holotype. **A, B, D, E,** pleopods, 1 to 3, 5, respectively; **C,** pleopod 2 endopod, proximomedial margin.

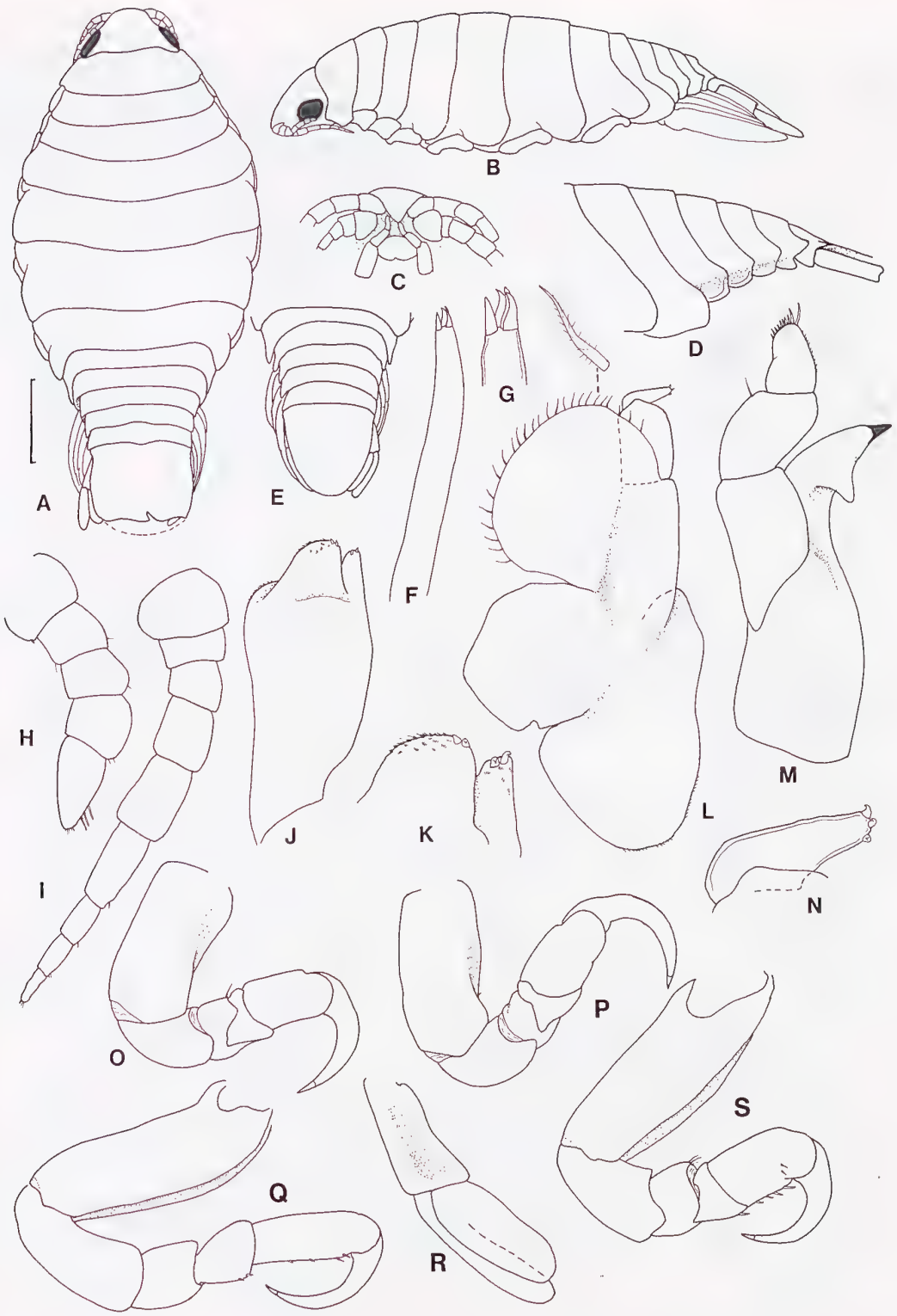

Fig. 31. *Anilocra pomacentri* n. sp., A–C, holotype; D,E, female 10.5 mm, Lizard Is. (AM P36270); remainder, female (11.0 mm, Wistari Reef (QM W12183). **A,** dorsal view; **B,** lateral view; **C,** frons; **D,** pleon, lateral view; **E,** pleon, pleotelson; **F,** maxillule; **G,** maxillule apex; **H,** antennule; **I,** antenna; **J,** maxilla; **K,** maxilla apex; **L,** maxilliped; **M,** mandible; **N,** maxilliped article 3; **O,** pereopod 1; **P,** pereopod 2; **Q,** pereopod 7; **R,** uropod; **S,** pereopod 6. Scale line represents 2.0 mm.

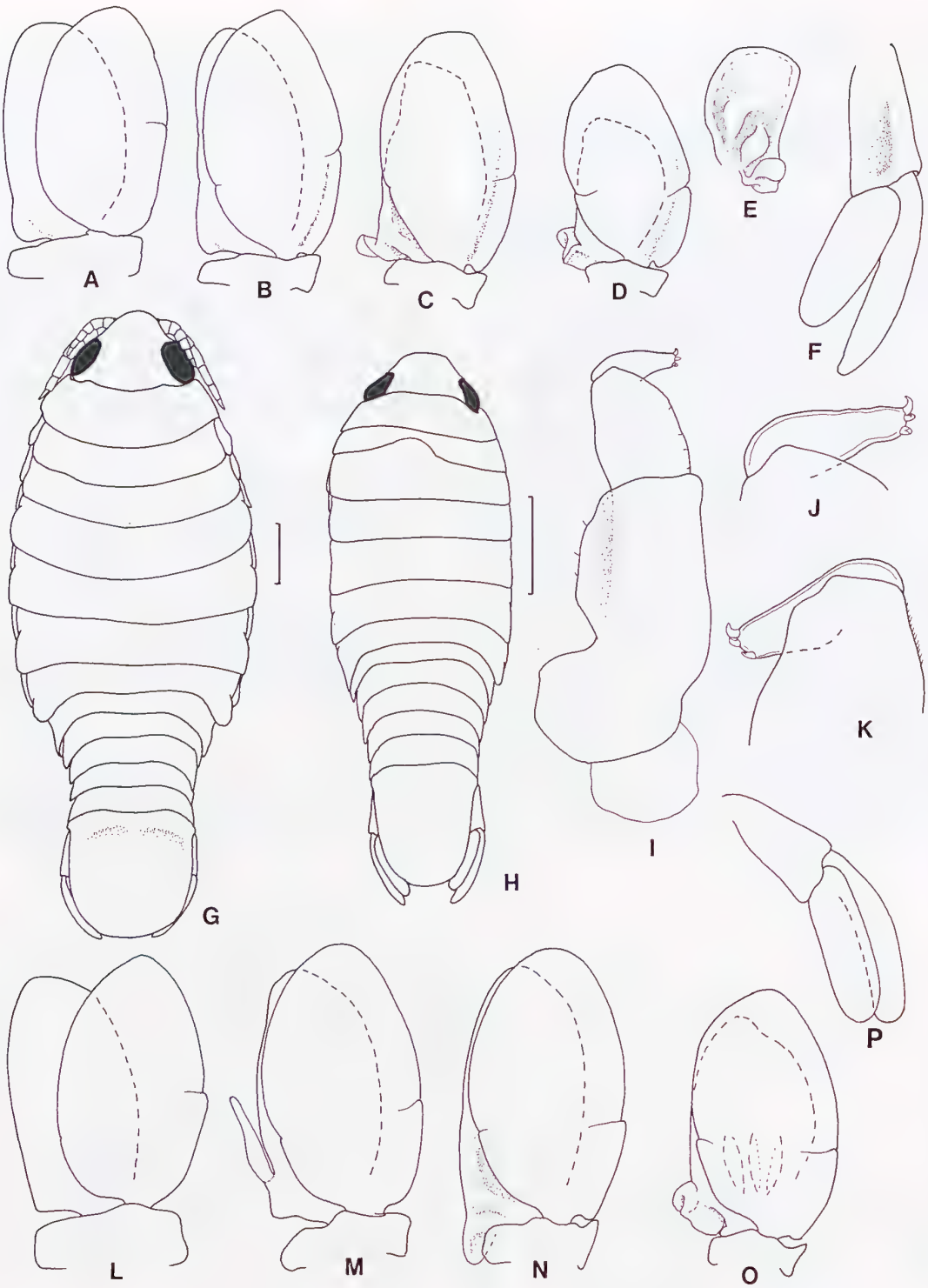

Fig. 32. *Anilocra pomacentri* n. sp., A–E, female 11.0 mm, Wistari Reef (QM W12183); F, female 9.5 mm, Wistari Reef (QM W12184); H, ?male 6.0 mm, Wistari Reef (QM W12184); remainder male 9.8 mm, Lizard Island (AM P36270). **A–D**, pleopods 1 to 3, 5 respectively; **E**, pleopod 5 endopod, posterior view; **F**, uropod; **G**, dorsal view; **H**, dorsal view; **I**, maxilliped, non-ovig female, Wistari Reef; **J**, maxilliped article 3, same; **K**, maxilliped article 3; **L–O**, pleopods 1 to 3, 5 respectively; **P**, uropod. Scale lines represent 1.0 mm.

Type locality. Wistari Reef, Capricorn Group, southern Great Barrier Reef, 23°29′S 151°53′E.

Description of female. Body about 2.0 times as long as wide. Cephalon with broad rostrum; eyes about 0.3 width of cephalon. Pc sterolateral angle of pereonite 1 weakly produced, forming rectangular lobe in lateral view. Pleonites subequal in length, posterolateral margins of pleonite 1 produced, those of pleonites 2–5 not enlarged, without acute dorsal posterolateral angles. Pleotelson flat, lateral margins curving smoothly to broadly rounded posterior margin.

Antennule with 7 articles, extending to mid point of

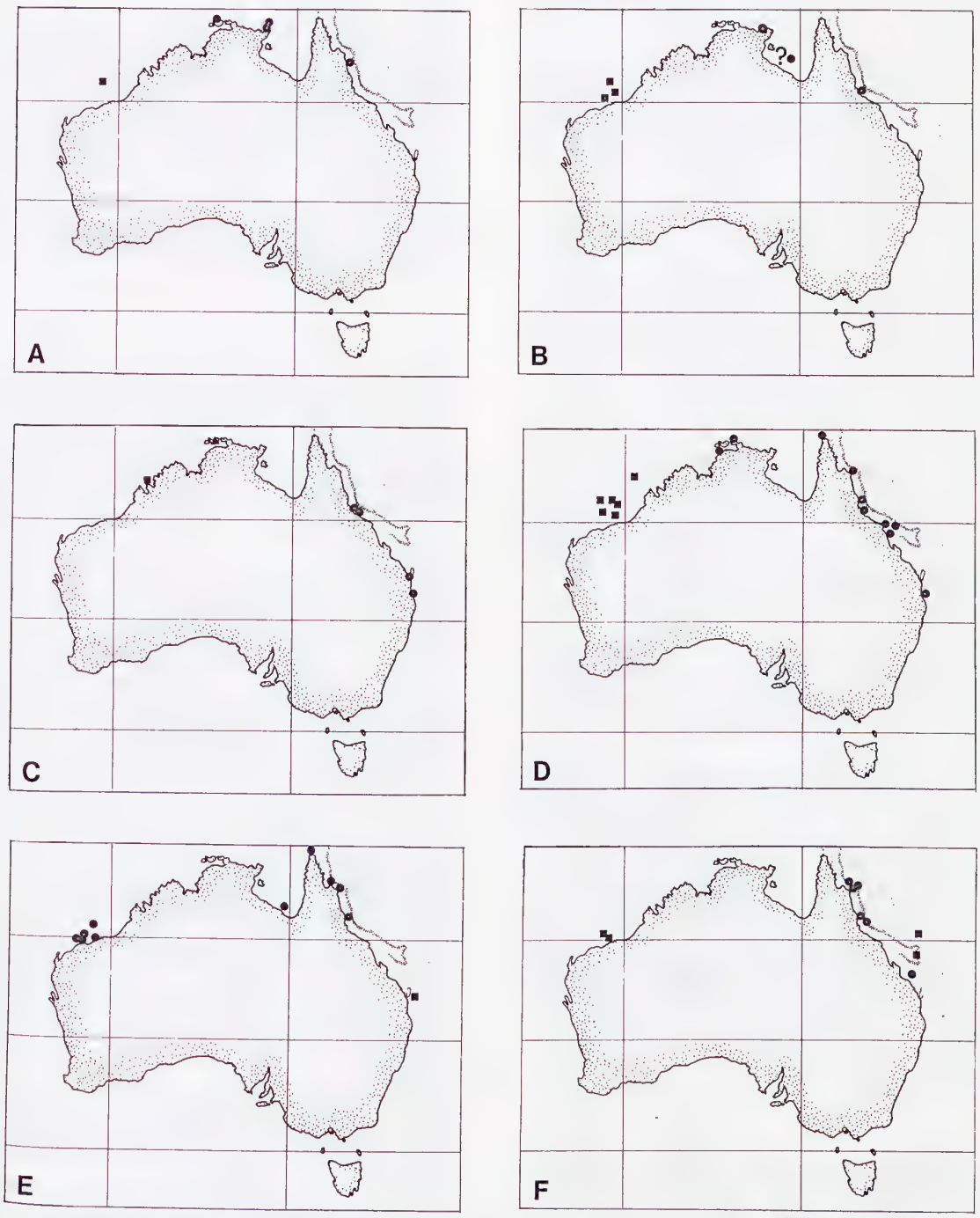

Fig. 33. Distribution of *Pleopodias* and *Anilocra* around the Australian coast. **A**, *Pleopodias* sp (■), *A. caudata* (●); **B**, *A. soelae* (■), *A. dimidiata* (●); **C**, *A. koolanae* (■), *A. leptosoma* (●), *A. alloceraea* (▲); **D**, *A. ankistra* (■), *A. apogonae* (●); **E**, *A. morsicata* (■), *A. nemipteri* (●); **F**, *A. longicauda* (■), *A. pomacentri* (●).

eye; article 3 anterodistal margin not produced. Antenna with 8–9 articles, extending to posterior of pereonite 1.

Mandible palp with about 12 setae on distal margin of article 3. Maxilla with 2 spines each on lateral and medial lobes respectively.

Pereopods 1–4 without nodules on dactylus; pereopod 1 dactylus robust, extending to carpus. Carpus and propodus of pereopod 6 with 1 and 4 small spines, pereopod 7 with 1 and 2 small spines.

Pleopods rami elongate; endopod of pleopod 5 with only 2 simple lobes; all exopods with proximomedial lobe, weakly developed on pleopods 1–2, prominent on pleopods 3–5. Uropod rami extending beyond pleotelson, exopod narrower and longer than endopod; apices bluntly rounded.

Male. Appendages similar to those of non-ovigerous female, but uropod rami subequal in length. Appendix masculina present.

Variation. Uropod exopod proportionally longer with more acute apex in non-ovigerous and immature female specimens. Antennule articles tending to fuse together; usually number is 7; antenna usually has 8 articles (7 of 9 cases). Adult females from the Palm Group have the anterior margin af the pereopod dactylus very slightly thickened.

Colour. Dorsum with dense chromatophores appearing dark brown to black, posterior of segments with thin clear band; chromatophores extending to antennule, antenna, ventral surfaces of cephalon, pereopods 1–7, pocket of brood pouch, peduncle of pleopod 1, and lateral margins of pleopods 1–4.

Size. Ovigerous females 11.0–12.5 mm, non-ovigerous females 6.0–9.8 mm.

Remarks. The lack of nodules on dactyls of pereopods 1–4, ovate body shape, flat pleotelson, and short rounded uropod rami are characters which serve to identify *A. pomacentri.*

Hosts. Recorded from *Chromis nitidus, C. atripes, C. margaritifer, Pomacentrus lepidogenys, Pomacentrus melanochir, P. Tamboinensis, P. melanopterus* and *P. moluccensis;* sight records on *Pomacentrus pavo* at Lizard Island and *Neopomacentrus violascens* at the Palm Islands. On the Great Barrier reef only one isopod per host was obseved, always situated dorsally above eye.

Distribution. Carter Reef, Waining Reef, Lizard Island, Palm Group, Myrmidon Reef, and Wistari Reef, Capricorn Group, all Great Barrier Reef.

Etymology. The name is derived from that of the most common host genus.

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References

Avdeev, V.V., 1975a. Two representatives of parasitic isopods of the genus *Lironeca* (Cymothoidae) from the region of Australia and New Zealand. Parasitologia 3: 247–251.

————1975b. A new parasitic isopod of the genus *Cterissa* (Crustacea: Cymothoidae) from the Sea of Timor. Biologia Morya 3: 69–73.

————1975c. A new parasitic isopod *Tetragonocephalon lutianus* gen. et sp. nov. from the Arafura Sea. Biologia Morya 5: 62–65.

————1977. Three new species of parasitic isopods (Flabellifera, Anilocridae) from the collection of the Laboratory of Parasitology of Sea Animals of TINRO. Fisheries, Oceanography, Hydrobiology and Fish Parasitology of the Pacific Ocean 1011: 139–144.

————1978. Notes on the distribution of marine Cymothoidae (Isopoda, Crustacea) in the Australian-New Zealand region. Folia Parasitologica (Prague) 25: 281–283.

————1979a. New species of the genus *Cymothoa* (Isopoda, Cymothoidae) from the coastal regions of north-western Australia. Parasitologia 13: 50–55.

————1979b. New species of the genus *Cymothoa* Fabricius (Isopoda, Cymothoidae) from the Indian Ocean. Parasitologia 13: 223–234.

————1979c. Parasitic isopods of the genus *Meinertia* from the Australian-New Zealand region. Biologia Morya 2: 48–54.

————1985. Specific features of the distribution of marine parasitic isopod crustaceans of the family Cymothoidae (Isopoda, Flabellifera). **In:** "Parasitology and Pathology of Marine Organisms of the World Ocean." (W.J. Harger, Jr ed.) National Oceanic and Atmospheric Administration. Technical Report, National Marine Fisheries Service 25: 1–135.

Barnard, K.H., 1925. Contributions to the crustacean fauna of South Africa. No. 9. Further additions to the list of Isopoda. Annals of the South African Museum 20: 381–410.

————1936. Isopods collected by R.I.M.S. *Investigator.* Records of the Indian Museum, Calcutta 38: 147–191.

Beumer, J.P., L.D. Ashburner, M.E. Burbury, E. Jetté & D.J. Latham, 1982. A checklist of the parasites of fishes from Australia and its adjacent territories. Commonwealth

Institute of Parasitology Technical Communication 48: i-vi, 1-99.

Bleeker, P., 1857. Recherches sur les Crustacés de L'Inde Archipelagique. II. Sur les Isopodes Cymothoadiens de L'Archipel Indien. Natuurkundige vereeniging in Nederlandsche-Indie, Batavia. Verhandelingen 2: 20-40, plates 1, 2.

Boone, P.L., 1935. Scientific results of the world cruise of the yacht *Alva* 1931, William K. Vanderbilt, commanding. Crustacea and Echinodermata. Bulletin of the Vanderbilt Museum, Huntington, N.Y. 6: 1-264, plates 1-96.

Bovallius, C., 1887. New or imperfectly known Isopoda. Part III. Bihang till Kongelige Svenska Vetenskapsakademiens Handlingar 18, 4: 1-21, plates 1-4.

Bowman, T.E. & I.U. Tareen, 1983. Cymothoidae of Kuwait (Arabian Gulf)(Crustacea: Isopoda). Smithsonian Contributions to Zoology 382: i-iii, 1-30.

Bruce, N.L., 1986. Revision of the fish parasitic isopod crustacean genus *Mothocya* Costa, in Hope, 1851 (Cymothoidae: Flabellifera). Journal of Natural History 20(5): 1089-1192.

Brusca, R.C., 1981. A monograph on the Isopoda Cymothoidae (Crustacea) of the eastern Pacific. Zoological Journal of the Linnean Society 73: 117-199.

Brusca, R.C. & E.W. Iverson, 1985. A guide to the marine isopod Crustacea of Pacific Costa Rica. Revista de Bilogia Tropical 33 (Supplemento 1): i-iv, 1-77.

Dana, J.D., 1853. Crustacea, Part II. **In:** "United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U.S.N." Volume 14, C. Sherman, Philadelphia, pp 689-1618.

Desmarest, A.G., 1825. Considérations génerales sur la classe des Crustacés. Paris, pp. xix, 446, 1 errata, plates 1-56.

Edwards, A.M., 1840. Histoire naturelle des Crustacés comprenent l'anatomie la physiologie et la classification de ces animaux. III, pp. 605.

Gerstaecker, A., 1882. Sechste Ordnung. Isopoda-Asseln [Part], pp. 97-278 **In** "Klassen und Ordnung des Thier-Reichs, wissenschaftlich dargestellt in Wort und Bild." (Dr H.G. Bronn ed.) Funfter Band II. Abtheilung. Gliederfüssler: Arthropoda. Crustacea. (Zweite Hälfte: Malacostraca) 4, 5, 6, 7, 8. Leiferung.

Hale, H.M., 1926. Review of Australian isopods of the Cymothoid group. Part II. Transactions of the Royal Society of South Australia 50: 201-234, plates 26, 27.

————1940. Report on the cymothoid Isopoda obtained by the F.I.S. *"Endeavour"* on the coasts of Queensland, New South Wales, Victoria, Tasmania and South Australia. Transactions of the Royal Society of South Australia 64: 288-304, plate 18.

Haller, G. von, 1880. Über einige neue Cymothöinen. Archiv fur Naturgeschichte, Berlin, Jahrbusch 46: 375-395, plate 18.

Herklots, J.A., 1870. Deux nouveaux genres de Crustacés vivant en parasites sur des poissons. *Epichthyes* et *Ichthyoxenos*. Archiv Neerlandaise Sciences exact et naturelle, 5: 120-137, plate 5.

Holthuis, L.B., 1978. Cymothoide isopoden van de Nederlandse kust en de Zuidelijke Noordzee. Bijdragen Faunisteit Nederland 5: 28-33, plate 1.

Kensley, B., 1978. Guide to the marine isopods of southern Africa. South African Museum, Cape Town, p. 173.

Koelbel, K., 1878. Über einige neue Cymothoiden. Sitzungsberichte der Mathematisch-Naturwiss enschaftlichen Klasse der Kaiserlichen Akadamie der Wissenschaften 78(1): 401-416, plates 1, 2.

Kussakin, O.G., 1979. Marine and Brackish water isopod Crustacea. Suborder Flabellifera Akademy of Science, U.S.S.R. Leningrad, pp. 470 [in Russian].

Leach, W.E., 1818. Cymothoidées. **In:** "Dictionnaire des Sciences Naturelle" (Cuvier, F. ed.). Volume 12: 338-354. Paris and Strasbourg.

Linnaeus, C. von, 1758. Systeme Naturale, 10 Edition, 1. Holmiae.

Miers, E.J., 1880. On a collection of Crustacea from the Malaysian Region - Part IV. Penaeidae, Stomatopoda, Isopoda, Suctoria, and Xiphosura. Annals and Magazine of Natural History 5, series 5: 457-467.

Monod, T., 1933. Mission Robert Ph. Dollfus en Égypt. Tanaidacea et Isopoda. Mémoires de l'Institute Égyptienne 21: 161-264.

————1934. Isopodes marins des campagnes du "de *Lanessan"*. Notes de l'Institute Océanographique de l'Indochine 23: 1-22, plates 1-45.

————1976. Expédition Rumphius II (1975). Crustacés parasites, commensaux, etc. (T. Monod & R. Sérène, ed.). III. Crustacés Isopodes (I[re] partie: Corallanidae, Anilocridae, Cymothoidae). Bulletin du Muséum National d'Histoire Naturelle, 3 série, 391, Zoologie 273: 853-870.

Nierstrasz, H.F., 1915. Die isopoden-sammlung im Naturhistorischen Reichsmuseum zu Leiden. - 1. Cymothoidae. Zoologische Mededeelingen, Rijksmuseum van Natuurlijke Historie te Leiden 1: 71-108, plates 3, 4.

————1918. Alte und neue isopoden. Zoologische Mededeelingen, Rijksmuseum van Natuurlijke Historie te Leiden 4: 103-142, plates 9, 10.

————1931. Die Isopoden der Siboga-Expedition. 3. Isopoda Genuina. 2. Flabellifera. Siboga Expeditie 32c: 123-233, plates 10, 11.

Pillai, N.K., 1954. A preliminary note on the Tanaidacea and Isopoda of Travancore. Bulletin of the Central Research Institute, University of Travancore, (C) 3: 1-21.

————1963. Two new genera of parasitic isopods from Kerala. Journal of the Zoological Society of India 15: 66-72.

Richardson, H., 1905. A monograph on the isopods of North America. Bulletin of the United States National Museum 54: 1-727.

————1910. Marine isopods collected in the Philippines by U.S. Fisheries steamer *Albatross* in 1907-1908. Department of Commerce and Labor, Bureau of Fisheries Document 736: 1-44.

————1911. Les crustacés isopodes du *Travailleur* et du *Talisman;* formes nouvelles. Bulletin du Muséum National d'Histoire Naturelle, Paris 17: 518-534.

Serène, R., 1937. Inventaire des Invertébrés marins de l'Indochine (I[re] liste). Notes de l'Institute Océanographique de l'Indochine 30: 1-83.

Schiödte, J.C. & Fr. Meinert, 1881. Symbolae ad monographiam cymothoarum crustaceorum isopodum familiae. II. Anilocridae. Naturhistorisk Tidsskrift Series III 12: 1-166, plates 1-10.

————1883. Symbolae ad monographium cymothoarum crustaceorum familiae. III. Saophridae. IV. Ceratothoinae. Naturhistorisk Tidsskrift, Series III, 13: 281-378, plates 11-16.

————1884. Symbolae ad monographium cymothoarum crustaceorum isopodum familiae. IV. Cymothoidae Trib.

II. Cymothoinae. Trib. III. Lironecinae. Naturhistorisk Tidsskrift Series III, 14: 221–454, plates 6–13.

Stebbing, Rev. T.R.R., 1900. On Crustacea brought by Dr. Willey from the South Seas. **In** "Zoological Results Based on Material from New Britain, New Guinea, Loyalty Islands, and Elsewhere, Collected during the Years of 1895, 1896 and 1897" (A. Willey ed.) 5(33): 605–690. University Press, Cambridge.

————1905. Report on the Isopods collected by Professor Herdman at Ceylon, in 1902. **In** "Report to the Government of Ceylon on the pearl oyster fisheries in the Gulf of Manaar". (W.A. Herdman ed.). Volume 4, Supplements report 23: 1–64.

————1924. Crustacea of Natal. Fisheries and Marine Biological Report No. 3 for the year 1922, 3:1–15, plates 11–16.

Trilles, J.-P., 1975a. Les Cymothoidae (Isopoda, Flabellifera) des collections du Museéum National d'Histoire Naturelle de Paris. II. Les Anilocridae Schiödte et Meinert, 1881. Genres *Anilocra* Leach, 1818, et *Nerocila* Leach, 1818. Bulletin du Muséum National d'Histoire Naturelle, Paris, 3^{e} série, 290, Zoologie 200: 303–340, plates 1, 2.

————1975b. Les Cymothoidae (Isopoda, Falbellifera) des côtes françaises. II. Les Anilocridae Schiödte et Meinert, 1881. Genres *Anilocra* Leach, 1818, et *Nerocila* Leach, 1818. Bulletin du Muséum National d'Histoire Naturelle, Paris, 3^{e} série, 290, Zoologie 200: 347–378, plate 1.

————1979. Les Cymothoidae (Isopoda, Flabellifera; parasites de poissons) du Rijksmuseum van Natuurlijke Historie de Leiden II. Afrique, Amerique et regions Indo-Ouest-Pacifique. Zoologische Mededeelingen, Rijksmuseum van Natuurlijke Historie te Leiden 54: 245–275.

Trilles, J.-P. & J.C. Vala, 1975. Sur trois espèces de Cymothoidae de la Gaudeloupe. Bulletin du Muséum National d'Histoire Naturelle, Paris, 3^{e} série, 318, Zoologie 225: 967–976.

Williams, E.H. Jr. & L.B. Williams, 1980. Four new species of *Renocila* (Isopoda: Cymothoidae), the first reported from the New World. Proceedings of the Biological Society of Washington 93: 573–592.

Williams, L.B. & E.H. Williams, 1981. Nine new species of *Anilocra* (Crustacea: Isopoda: Cymothoidae) external parasites of West Indian coral reef fishes. Proceedings of the Biological Society of Washington 94: 1005–1047.

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The Devonian Dipnoan *Holodipterus:* Dental Form Variation and Remodelling Growth Mechanisms.

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ABSTRACT. The dentition of the Late Devonian *Holodipterus gogoensis* Miles (Osteichthyes: Dipnoi) is described from the original material and four new specimens. Variation between specimens is considerable because growth took place in cycles that involved extensive resorption of tissues of all types on the dental surface, followed by periods of reconstruction during which new distributions of hard tissues were established. The teeth have an enamel cover and a hard compact dentine core within which an unusual interstitial material is present. They were added alternately to the lateral margins of the pterygoids and the prearticulars. In this way new teeth were always added outside the occlusal surface. Enlarged marginal denticles around the edges of the bones provided a surface to protect against wear by opposing teeth during the growth of the new teeth on the opposing jaws. The surfaces of the pterygoids and the prearticulars were partly covered with superficial denticles that were shed individually, or episodically in large numbers during phases of total resorption at an advancing front. Isolated denticles were also shed and regrown independently of those around them. After the episodic resorption, newly formed denticles were gradually embedded in, and in some places overgrown by, a layer of simple superficial dentine. This was then invaded by hard pleromic dentine. The next resorption phase did not remove all this dentine, and callosities of hard, compact dentine remained to continue pleromic growth into the palate. The generic relationships inferred from this unique dental pattern are discussed. A consideration of the complex of features forming the feeding apparatus leads to the conclusion that *Holodipterus* shares more characters with members of the denticulate dipnoan lineage than the tooth-plated lineage. However, characters shared with the primitive tooth-plated genus *Speonesydrion* may be significant. Further information on the dental structure of some other genera, particularly *Fleurantia,* is required before more definite conclusions can be reached.

CAMPBELL, K.S.W. and MOYA M. SMITH, 1987. The Devonian dipnoan *Holodipterus:* dental form variation and remodelling growth mechanisms. Records of the Australian Museum 39(3): 131–167.

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This work is dedicated to the memory of E.S. Hills, formerly Professor of Geology at the University of Melbourne, who died in 1986. In the Records of the Australian Museum, Volume 21, 1941, he published a paper on the primitive Devonian lungfish *Dipnorphychus sussmilchi* (Eth. fil) which initiated a new phase of palaeontological study of the Dipnoi in Australia and overseas.

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Holodipterus has one of the most unusual of all known lungfish dentitions. It has large, enamel-covered, radially arranged teeth around the margins of the pterygoids and the prearticulars, and extensive areas of the surface of these bones are covered with denticles that were shed and regrown at irregular intervals (Miles, 1977; Smith, 1977; Campbell & Barwick, 1986). Thus it has the dental characteristics of the two groups of dipnoans - one, such as *Dipterus,* that crushed and triturated its food, and the other, such as *Griphognathus,* that depended largely on a shagreen of denticles lining the buccal cavity for the manipulation and any necessary reduction of food without crushing and triturating.

Several questions arise immediately. Are there really two discrete types of dentition that define separate evolving lineages, or does *Holodipterus* provide evidence of a true intermediate morphology? Is it possible, therefore, that tooth plates do not define a monophyletic group as has been proposed by many workers (Denison, 1974; Miles, 1977; Campbell & Barwick, 1983)? If *Holodipterus* is not a tooth-plated type, but a denticulated type that has secondarily produced a plate-like structure (Campbell & Barwick, 1987), what kind of evidence from development and histology would permit the recognition of simulated tooth plates?

As part of a review of Palaeozoic and Mesozoic dipnoan dentitions we have reinvestigated *Holodipterus gogoensis* from new and previously

described material. Representatives of this species are not common and specimens available for histological sections and for scanning electron micrography are at a premium. We are grateful to Dr Peter Forey, of the British Museum (Natural History), London, for making part of a palate available to us for these purposes, and Dr Gavin Young, of the Bureau of Mineral Resources, Canberra, for allowing us to etch and section specimens in his care.

MATERIALS AND METHODS

All the specimens examined are from the Gogo Formation of the Canning Basin, Western Australia. This is of Frasnian (Late Devonian) age. They have been prepared by etching from limestone nodules with acetic acid. Thin sections have been cut from some of this prepared material and some of it has been used for scanning electron micrograph (S.E.M.) work. The photomicrographs and the S.E.M.'s in Figures 10–18 are from vertical sections cut in a labio-lingual plane through the marginal tooth on the anterior row of the pterygoid (CPC25738). All S.E.M's in Figures 15–18 are from the block face immediately adjacent to the section (Fig. 10) polished and etched for 1 min. with normal H Cl.

A small fragment of the palate of CPC25738 was not etched, and this has been sectioned and scanned. We draw attention to the fact that by far the best histological detail is obtained from unetched material. This is because the etched material has to be impregnated with a mounting medium that may not completely fill the pore spaces, the walls of which may then collapse during sectioning. Of greater significance is the point that if the specimen is sectioned with the carbonate matrix in position, the birefringence of that mineral helps define the outlines of the biological tissues under crossed polars, and subtle details are revealed by examination in ultraviolet light.

We have examined all the specimens housed in the British Museum (Natural History) that were used by Miles (1977: 14) in his original description of the species. Details of specimen numbers and locations may be obtained from that publication. In this work, the B.M. (N.H.) specimens are indicated by the prefix 'P'. Four new specimens in the Commonwealth Palaeontological Collections, indicated by the prefix 'CPC', have also been used. They come from the holotype locality at Paddy's Springs.

GROSS MORPHOLOGY

The broad outlines of dental morphology have been provided by Miles (1977: 209–214, 294–296; Figs 4a,b, 40, 108–110). The most striking feature of his specimens is the range of variation they exhibit, and this has been increased by the addition of the four new specimens CPC25738–CPC25741 (Figs 1, 3, 19). The palates are highly arched, and occlusion takes place only around the labial margins. It is surprising, therefore, that a hard, dark-coloured, irregularly shaped, dentine mass always stands proud of the surrounding tissues on the median posterior part of the palate, and a similar but smaller median anterior mass is present on some specimens (Figs 1; 2; 4A; 5A,B). The posterior mass, hereinafter referred to as a callosity, is either simple, or extended anterolaterally to form ridge-like features that tend to align with the first or the second marginal tooth rows. These ridges are composed of continuous hard dentine, or two or three more or less discrete knob-like masses. The marginal teeth are always present, and either overhang the labial edges of the pterygoids or lie within their margins. The number of teeth in each row varies between specimens or even on opposite sides of the one specimen. Denticles cover large areas of the surface, or they are restricted to small patches, whereas the remainder of the surface is covered with a sheet of a relatively dense substance referred to by Miles (1977) as dentine.

Similar kinds of statements may be made about the mandibles (Figs 3A,B; 6A; 7A). The marginal teeth lie within or overhanging the labial edge of the prearticular, and the number of teeth in the tooth rows varies. The size and shape of the mass of dentine on the heel of the 'tooth plate' differs even on opposite sides of the one specimen, as also does the area covered by denticles. And finally, two specimens (P52565 and CPC25341) show the superficial sheet of dentine covering almost the entire buccal surface of the prearticulars (including the depths of the lingual furrow), the surface of the adsymphysial plate and the adjacent parts of the dentary, whereas P56045, which is almost exactly the same size, has exposed bone over the floor of the lingual furrow. The dentary on CPC25738 has a row of small teeth along the lateral crest (Figs 3A,B; 4D). Flanking this row on the outer side is a new layer of dentine on which new teeth are not developed.

These observations pose the fundamental question – is the variation the result of individual differences, or of a massive reorganisation of tissues undergone by all members of the species during growth? The answer to this question determines our understanding of the phyletic position of the genus.

The first point to make is that there seems to be no correlation between structural differences and specimen size. If this had been so, the matter would have been easily resolved. However, the absence of a correlation may mean that remodelling of the dental surface took place many times during the life history of a single animal, and that these processes extended well into the adult stage. Consequently, if the observed variation is to be interpreted as the result of death at various stages of the remodelling process, it is necessary to find evidence of resorption and redeposition of dental tissues at both the macroscopic and microscopic levels. For these purposes the

following structures were examined: marginal teeth, denticles, basal bone, surface sheets of dentine, and dentine callosities of the palate and prearticular.

Marginal Teeth

These are large conical bodies that are almost right-circular when free standing, but more commonly slightly compressed when closely juxtaposed to the previous member of their row. A maximum of four occur in any one row, and this is on the lingual row of the mandible P50197. Most rows have only two teeth, and the more posteriorly placed teeth are single. The most labial tooth in a row is invariably the largest and the most complete, those on the lingual side being progressively more worn. There is also a decrease in size of the component teeth from anterior to posterior along the pterygoid. The tooth rows are aligned so that the whole array of rows on a single pterygoid never covers an angle of more than about 70°.

The isolated and unworn teeth have an enamel external coating, and show evidence of being fluted around the base as a result of slight infolding of the basal dentine. Clearly they were formed in an epithelial invagination in the same manner as the teeth of *Dipterus* and *Sagenodus*. However, the conformation of the dental surfaces is such that if the highest tooth in the row is on the labial end, it must

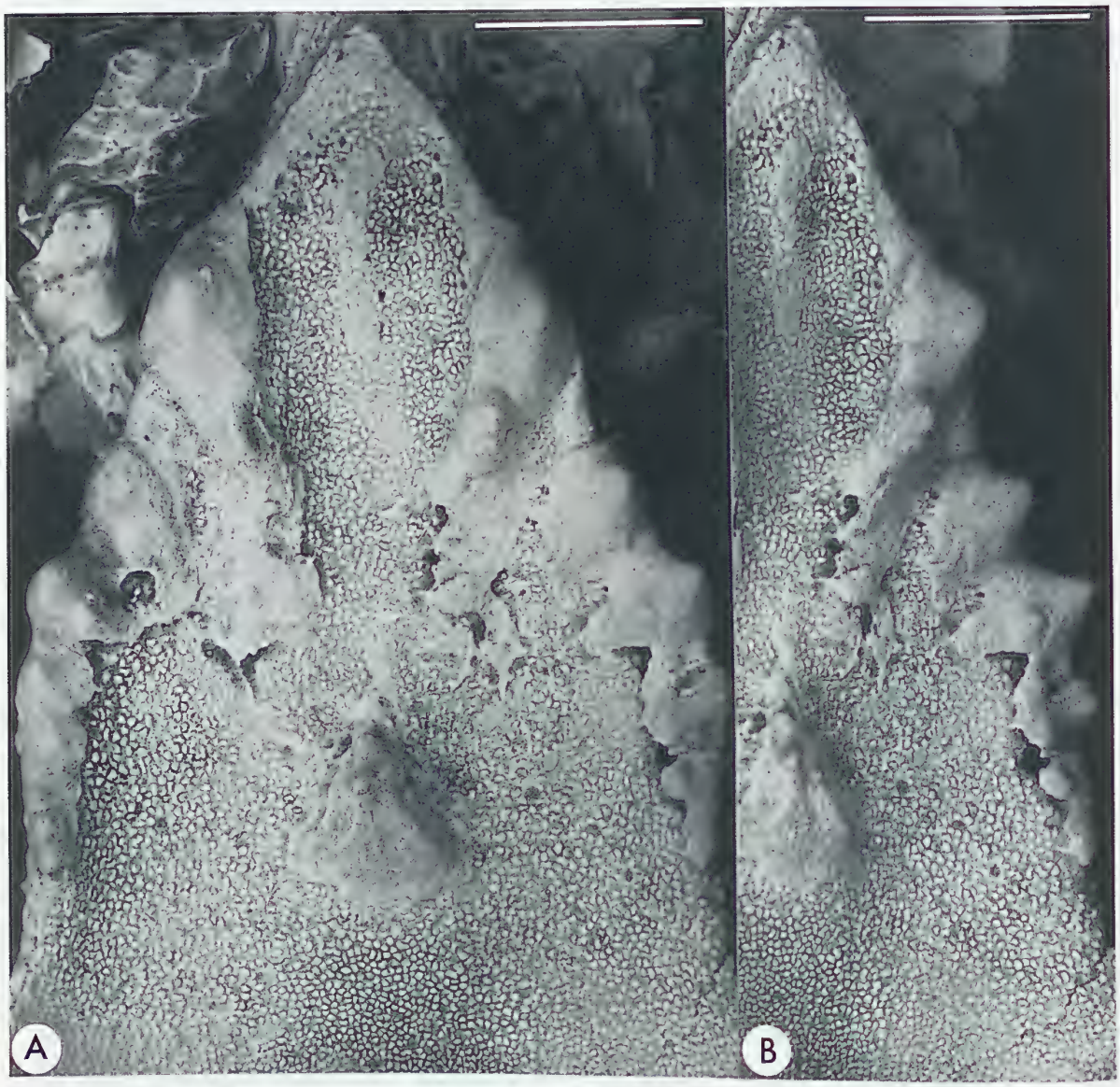

Fig. 1. (Scale bars = 10 mm). **A,B:** Ventral and ventromedial views of the palate of the smallest specimen available, CPC25740. Note the extent to which resorption of the superficial layer has taken place, and the way this has undercut the teeth, the resorbed surface being covered with new denticles.

have reached its fully formed shape and position by one of three modes. (a) The developing teeth in the two plates would be in opposing positions, but at a low level and out of the bite. They would move into the bite by appositional growth of dentine and bone at their bases. This seems to be the mode adopted by *Dipterus* and *Sagenodus*. (b) The developing teeth would be initially positioned as above but would come into the bite by means of wear on previously formed teeth in the same row. This effectively causes rotation of the occlusal plane relative to the base of the plate; dentine then would have to grow basally, into the bone, to maintain plate thickness. (c) The teeth of one plate would be formed outside the lateral margin of those in the opposing plate and at the same level as the previously formed tooth in the same row. By appositional growth of bone and dentine at their bases such newly formed, unopposed teeth would then have grown taller than previously formed ones.

Modes (a) and (b) receive no support from our observations, but mode (c) is substantiated by two unequivocal pieces of evidence. Two articulated individuals (P52568 and CPC25738) show the outer teeth on both mandibular rami lying outside the palatal marginal teeth (Figs 3D; 8); and, as noted above, one palate (Fig. 4A) and one mandible (Fig. 6) show the marginal teeth overhanging the edges of the bone on which they lie.

This mode of growth clearly implies that tissue was added along the labial margins of both pterygoids and prearticulars, and that little if any addition took place along the median line. Consequently, it is surprising to find that the tooth rows are so short and consist of so few elements. If growth were continuous radially, one would expect to find many worn teeth forming each row as is normal for dipnoan tooth plates. Moreover, the smallest known palate, CPC25740, has the same number of rows and the same number of teeth as the largest ones, though it is only about two thirds their size. The only conclusion that can be drawn from these data is that teeth on the palate were progressively lost from the lingual ends of the tooth rows as new ones are added to the labial margins. This, however, does not apply so uniformly to the tooth rows of the lower jaw in which resorption was not so extensive (see below).

These surprising conclusions are substantiated by an examination of the holotype (P52569) and CPC25740. On the holotype, a tooth of the third row on the left side is almost completely undercut, but has not been lost (Fig. 2A,B). The process of resorption was not completed before the next phase of tissue deposition began (see below). In addition CPC25740 shows extensive undercutting of the teeth of the third and subsequent rows on both sides of the palate (Fig. 1A,B).

When resorption was complete, even the thickest dentine forming the cores of the palatal teeth was removed. Because of the scarcity of material we are unable to demonstrate this by sections along the axis

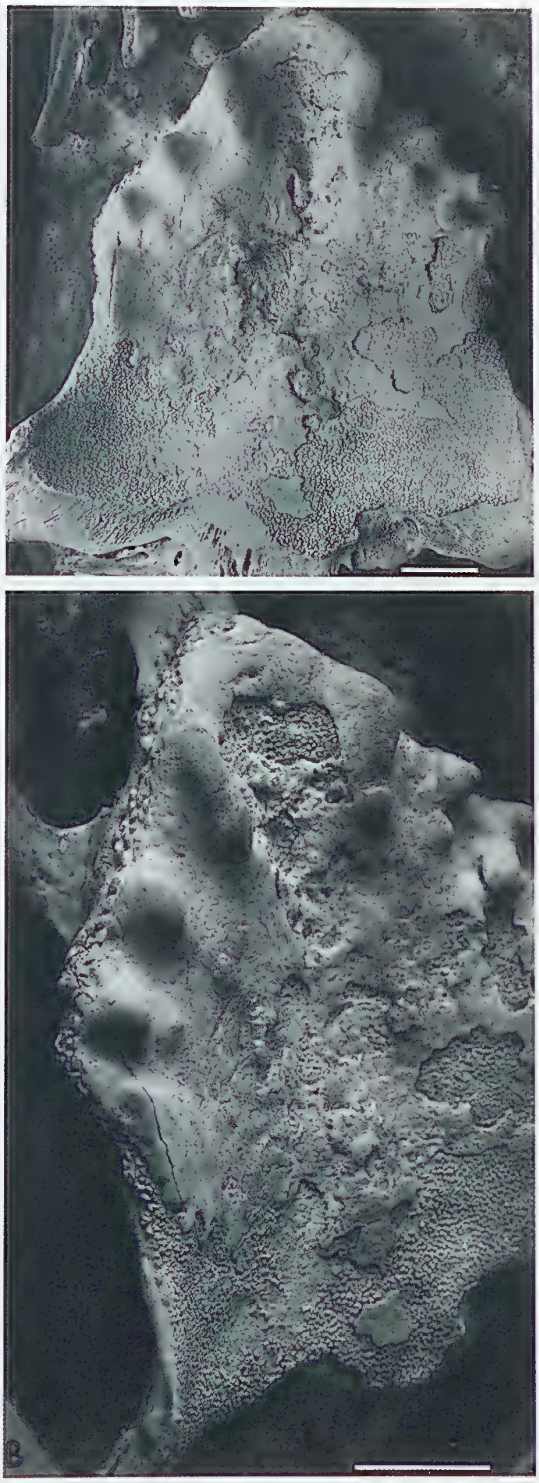

Fig. 2. (Scale bars = 10 mm). **A,B:** A larger specimen, P52569, of the palate in ventral and ventromedial views. Note in B, the numerous marginal denticles extending beyond the teeth, the superficial layer completely covering the bases of the teeth, and the denticles over large areas of the pterygoid. One of the teeth in the third row on the right side of the photograph in B has been undercut, and a new superficial layer had been deposited when the animal died.

of a tooth ridge, though vertical transverse sections of the palate of CPC25739 show no sign of buried teeth in the position expected to be occupied by older teeth (Fig. 19C,E). In addition, P56045 shows a gap in the palatal surface where the second tooth of the third ridge has been shed, the floor of the gap now being occupied by newly formed denticles attached to new bone (Fig. 4A,C). Evidence of this type is as adequate as evidence from sections. Removal of all the tooth cores on the prearticulars was probably not so complete, and they may have contributed to further pleromic growth to produce a tooth plate-like structure (Figs 6A; 7A). However, it remains true that some of the radial ridges on the prearticulars are not developed from worn teeth because large specimens (P56045, CPC25341) have a ridge deep in the lingual furrow where no teeth ever existed (Fig. 6A).

The largest teeth are always at the anterior end of the lingual row. In the lower jaw, this largest tooth always lies immediately behind the posterolateral end of the dentary (Figs 3A; 4D). This means that new teeth were not added to the lingual row without considerable bone growth at the edge of the prearticular along its junction with the dentary, and marked lateral growth of the posteriorly directed parts of the dentary. As the suture between the prearticular and the dentary was kept open, there would have been no difficulty in producing prearticular growth of this kind. However, there is no median suture in the dentary, and hence lateral growth of that bone must have resulted from resorption along its junction with the prearticular and lateral deposition along the edge forming the margin of the labial furrow. This is well shown on Figure 4D. This complex mode of growth of the dentary apparently took place relatively slowly, because there is clear evidence that teeth were not added at the end of the lingual row at the same rate as at the ends of the more posterior rows. This evidence is best illustrated by reference to the palate (see Fig. 9). The smallest palate has an acute anterior terminus and a broadly convex lateral margin. Progressively larger palates have anterior angles increasing to almost a right angle, and their lateral margins are straight as far back as the end of the third or fourth tooth ridge at which point the width is abruptly constricted. Given that the most anterior tooth remains the largest, this change in palatal proportions can result only from the addition of marginal teeth progressively more frequently at the ends of the second, third and fourth rows.

Denticles

Denticles are found on two distinct areas: across the buccal surfaces of the pterygoids and prearticulars – superficial denticles; and along the steep labial margins of the teeth in both jaws – marginal denticles.

Superficial denticles. The denticles of this group vary greatly in shape from simple cones to complex multi-ridged forms with many separate points on the ridges (Smith, 1977: figs 58, 64). These are quite comparable in shape with those of *Griphognathus whitei* (Smith, 1977: figs 44–49; Campbell & Barwick, 1983: figs 18–19). Specimen P52569 is unusual in that on the posterolateral part of the palate many denticles are more or less equidimensional in outline at their bases, but rise to a single, sharp crescentic edge (Fig. 4B). A similar pattern occurs on the prearticular just in front of the glenoid fossa on P52569 (Fig. 5D). On all specimens old and new denticles occur on the same surfaces. This implies that replacement of denticles took place irregularly throughout the growing process, and was not restricted to separate phases. This process of replacements is of the same type as that observed in *G. whitei*. A denticle grew till it reached the wear surface and its enamel cap was gradually removed by wear. After a short period the denticle was shed, leaving an exposed concave resorption surface within which a new denticle appeared. These details have been reported and photographed previously (Smith, 1977: figs 58, 64, 65).

Such denticles grew only on new bone, details of which are given below. They appear a short distance behind a resorption edge as is well shown on the mandible of P52569 where new bone may be observed in a narrow strip in such a position. This resorption edge lies in a superficial layer of white dentine that incorporated a previous generation of denticles (Fig. 5D). From these observations it can be seen that denticles provided the first cover on all those parts of the buccal surface from which old tissues had been removed. New denticles also formed on the prearticulars in the median symphysis where new bone was added during growth. This is well shown on P50197 and CPC25738.

Marginal denticles. These denticles are present on the labial sides of the teeth only if the specimen was not in the process of adding new teeth. Presumably once a new tooth was fully formed and the supporting bone had grown laterally beyond its outer margins, new denticles appeared in the region temporarily out of occlusion. Their crests were subsequently worn because they must have acted to protect this new bone from wear by the action of the newly formed teeth of the opposing jaw (Figs 2B; 7; 8).

Though these denticles show some irregular shapes, a high proportion of them are more regular in form, being approximately oval or triangular in plan. They also have several other distinctive features that provide clues to the mode of growth of the whole dental apparatus of the genus. Specimens P52565, P52569 and CPC25341 are of particular significance. The right side of P52569, a palate, has a large number of newly formed denticles around the margin (Fig. 2B). They are most abundant in the spaces between the ends of the teeth, which is what would be expected if they served the protective function mentioned

Fig. 3. (Scale bars = 10 mm). **A,B:** Dorsolateral and dorsal views of a mandible, CPC25738. **C:** Ventral view of the palate of the same specimen. The missing tooth from the anterior ridge is the one that has been sectioned and scanned. **D:** Dorsal view of the palate superimposed on the mandible in its natural position to show the occlusal relationships. Note the teeth on the right of the mandible more newly formed, biting outside those of the palate and not surrounded by marginal denticles.

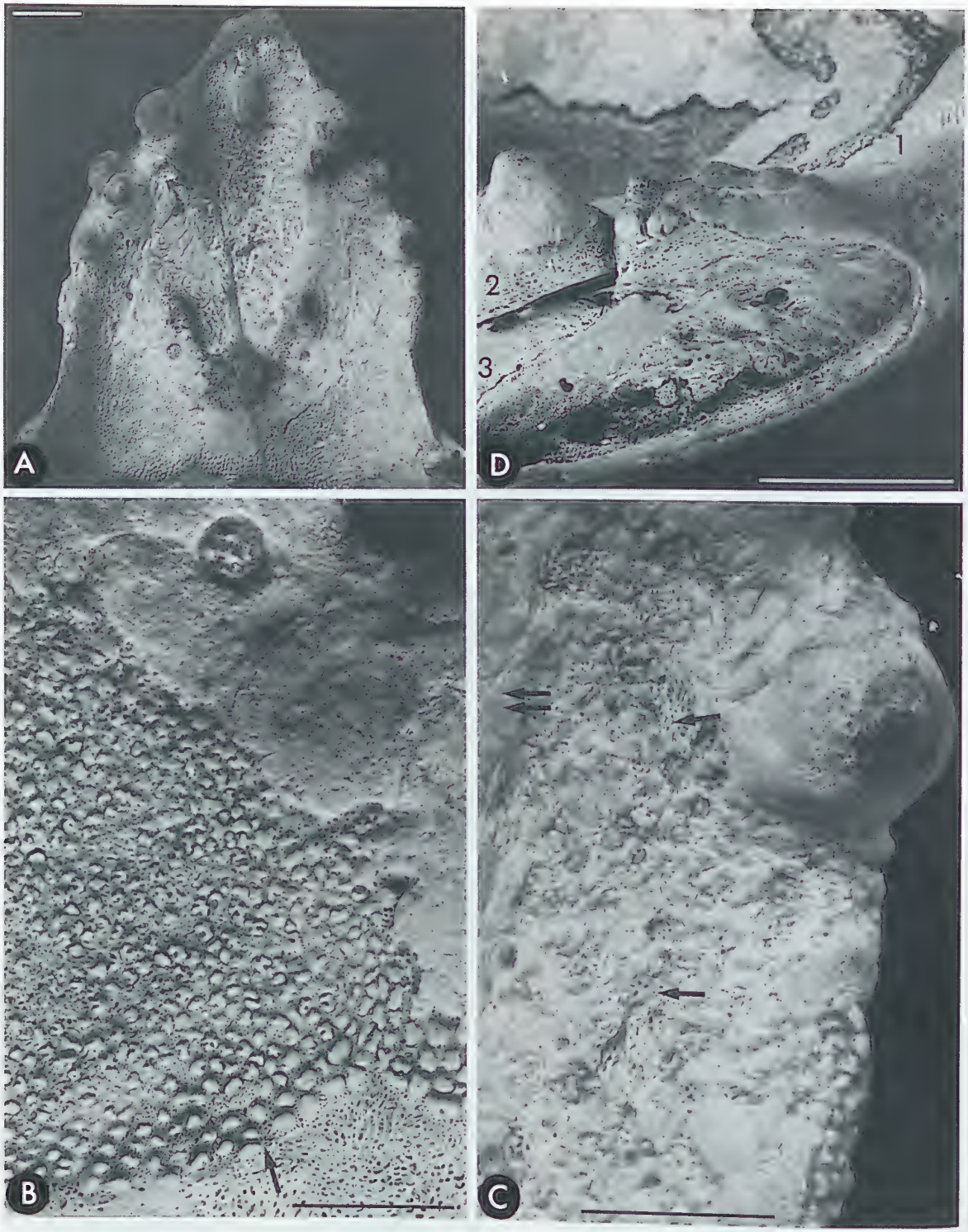

Fig. 4. **A:** (Scale bar = 10 mm) Ventral view of a palate not whitened with NH 4 Cl. The dark colour of the hard compact dentine of the callus and the teeth shows up clearly. The superficial dentine was in an expanding phase. **B,C:** (Scale bars = 5 mm). **B:** Right posterior part of palate. Note the fine new bone (arrow) over the coarse old bone of the parasphenoid and the adjacent pterygoid; the circular patch of denticles that was being encroached upon by the superficial dentine layer; and the variety of shapes adopted by the denticles. **C:** The surface adjacent to the most lateral tooth on the left side of the palate. Note the central core of dark compact dentine, the less mineralised layer around it, and the superficial dentine layer. Medial and posterior to the tooth is a strip on which the basal bone is exposed in places (single arrow). On it there are numerous denticles between which new superficial dentine was growing. A complete sheet of this dentine has overgrown the denticles in one area (double arrow). **D:** (scale = 5 mm) Dorsolateral view of the labial pit and surrounding areas of the mandible, CPC25738. Note the lateral growth on the dentary, the relationships of the dentary (1), prearticular (2) and angular (3) bones around the cartilage bone forming the floor of the labial pit, and the longitudinally grooved base on the anterior prearticular tooth. A-C: P56045

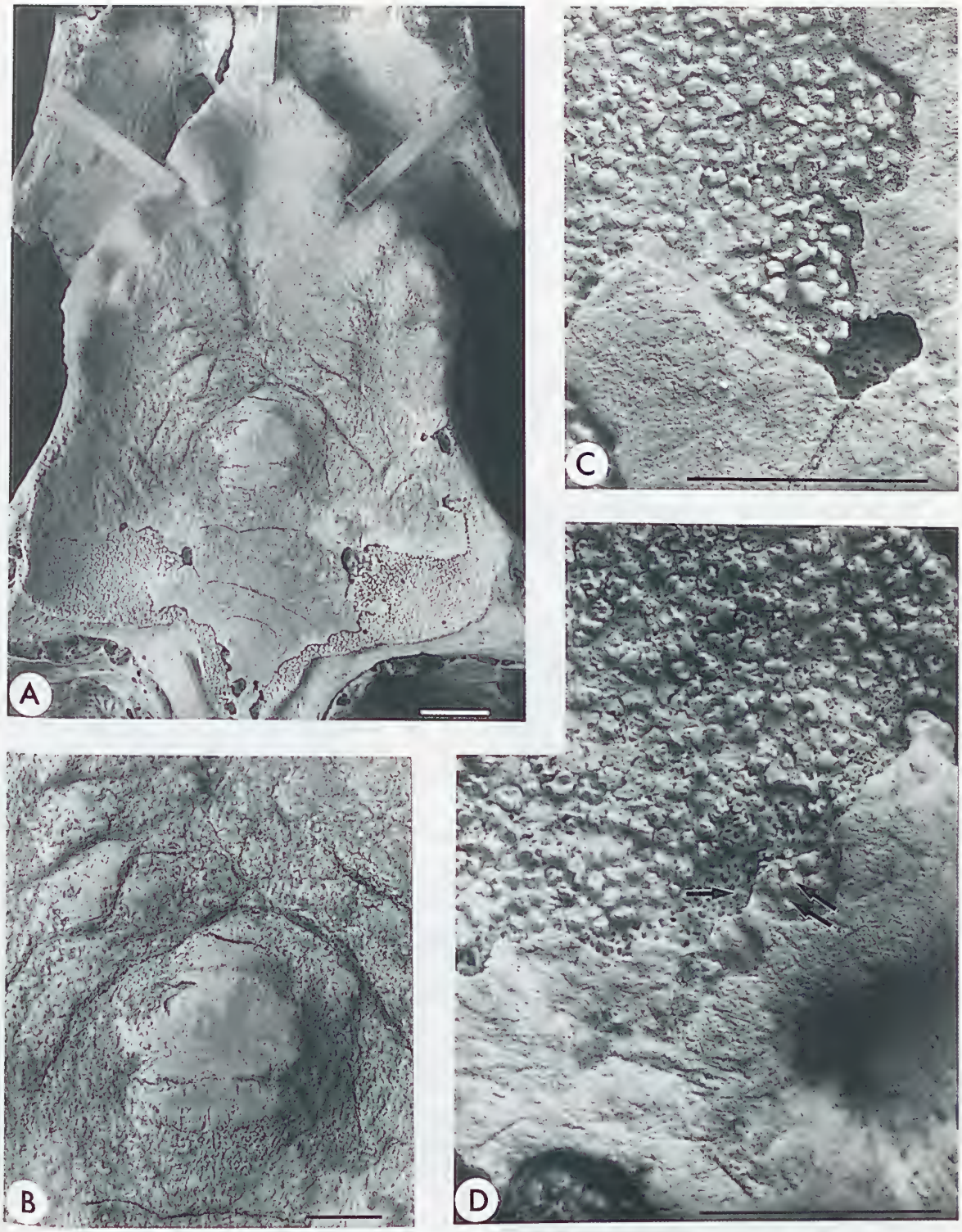

Fig. 5. (Scale bar of A = 10 mm; B–D, = 5 mm). **A:** Ventral view of a large palate, P50999; the individual died at the beginning of the resorption phase. Note the sub-concentric subdivisions of the old superficial layer producing pseudo-tooth ridges. In **B** these and the posterior median callosity show a polished surface. **C:** Right posterior part of palate of Figure A, slightly rotated clockwise, and showing denticles and a new deep resorption pit that has removed some denticles and part of the superficial layer. **D:** right posterior part of a mandible, P52569, showing a variety of denticle shapes, and a resorption edge behind which a strip of bone (arrow) is exposed, and in front of which the continuous sheet of old superficial dentine and a previously formed patch of denticles (double arrow) were in the process of being resorbed during a previous resorption phase.

above. Individual denticles are elongate in outline but those along the outer margins show radial struts around the bases of their labial faces where they can be seen attached to the basal bone. The occlusal and lingual edges of these denticles are all invested with the superficial layer of white dentine. Denticles still closer to the biting edge of the palate are completely surrounded by new bone and have become incorporated into the palate (Fig. 7C). The tops of the denticles are almost all worn, indicating that they became functional shortly after they appeared. There is no evidence of shedding, at least in the region of the major teeth.

The right side of specimen P52565, a mandible, shows a different stage in the development of these denticles (Fig. 7). Most of them are ovate in outline and are worn on top. Even those in the most labial position do not have exposed bases, but are partly encompassed by new trabecular bone (Fig. 7C). This bone has grown over the enamel coating of the denticles. Some of those in a more occlusal position are almost completely covered by new bone. Denticles at the labial margin in the furrows between the teeth are engulfed by the white superficial dentine. A similar pattern is shown on the right ramus of CPC25341.

We conclude from study of these specimens that new denticles were added to the labial faces of the pterygoids and prearticulars after new teeth had been added and new bone had grown out to the level of the labial margins of these teeth. Denticles developed in the same way as the superficial denticles of the palatal surface, but as they reached full size new bone began to grow over them and they became completely incorporated within the pterygoid or the prearticulars. Though none of them was shed, they rapidly lost their identity once they were incorporated in the newly formed bone (Fig. 24A). New denticles were added while the bone grew slowly outwards until the phase was reached when new teeth were to be added. As is shown in Figure 7B,C, bone was then laid down relatively rapidly while denticle formation was in abeyance.

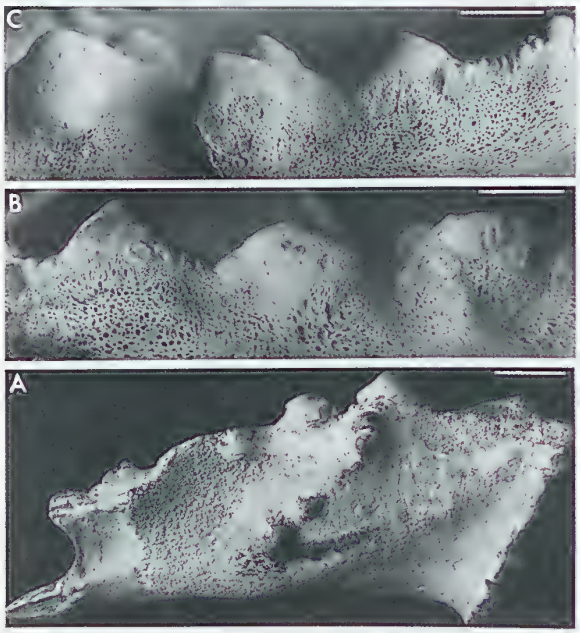

Fig. 6. **A:** (Scale = 10 mm) Left prearticular, P56045, with median symphysis on right, without NH_4Cl coating. Note dark coloured compact hard dentine, especially the ridge in the lingual furrow where no teeth were developed, and absence of denticles in the floor of the lingual furrow. **B,C:** (Scales = 5 mm) Lateral views of the prearticular teeth of same specimen. Both show a stage where new teeth have been added completing a new phase of addition but without new marginal denticles.

Basal Bone

The palate of this genus is unusually thin for a form that has so large a head. Its greatest thickness is lateral in position (Fig. 19C,E) where there is need to support the lateral teeth. No lateral palatal 'process' is present in that region but a long palatal ridge is developed in its place. In front of the parasphenoid the median part of the palate is thin.

Polished surfaces show that the palatal thickening took place by addition to its dorsal surface where increments are represented by sharply defined growth layers. Beneath these layers, particularly beneath the lateral palatal ridge, the bone has been resorbed and remodelled to allow the passage of vessels and nerves in the manner described and illustrated by Miles (1977: fig. 71). This bone is formed of large trabeculae that produce a very open texture. It is not represented medially. Beneath the teeth the bone has a more compact structure than that elsewhere on the palate. Towards the mid-line this tissue thins out except where a median callosity is present. The extensive resorption of bone that has taken place, as well as the resorption of the superficial dentine, is well illustrated in Figure 19D,F. The growth layers that form the dorsal part of the lateral palate were progressively resorbed towards the mid-line, and bone is exposed on the palatal surface except where the truncated ends of the bone trabeculae are covered with a new thin growth of superficial dentine or denticles.

Very finely trabeculated new spongiosa was formed on the old resorption surfaces prior to denticle formation (Fig. 4B). This is comparable with bone of attachment frequently formed with teeth or denticles.

Superficial Dentine Layer

This material covers a great deal of the surface at various stages of growth. It expands centrifugally. On several specimens (P56045, P52561) it is observed to have formed in advance of its continuous margins by

the development of narrow, isolated patches on the bone between denticles (Fig. 4C). These patches then coalesced and thickened, gradually burying denticles. Elsewhere, tissue of the same kind is found covering the enamel around the bases of the teeth on the lingual side. In addition, on several specimens it grew over the edge of the pterygoid, around the base of the marginal teeth, enveloping the denticles on the labial face of the bone. Its forming surface was not completely smooth; subsequent wear has abraded both this dentine and the associated denticles down to the level where the internal structure of the denticles can be clearly seen (Fig. 7B,C).

The tissue was temporary; some specimens show destructional and others show constructional edges. At resorption (destructional) edges the dentine sheet is often deeply undercut to expose a strip of fine-textured bone (Fig. 5D). At most locations a new generation of denticles lying well below the level of the functional surface borders the edge of this strip. Only in the lingual furrow of P56045 is there a considerable area of exposed bone and only a few scattered denticles left by resorption of the overlying tissue sheet (Fig. 6A). This indicates a complete removal of the superficial dentine layer.

The superficial dentine developed as a covering layer on this fine-textured bone between the denticles. It consisted of thin spurs of dentine which gradually united with adjacent spurs, as can be well seen on P56045. These produced a more open texture than the underlying bone. With increasing age the spaces were gradually infilled by concentric layers of similar tissue until a continuous non-porous sheet was developed.

This dentine layer completely covered old denticles and encroached over the bases of the teeth and callosities. A fine example of this is the undercut tooth on the holotype palate, which has the gap beneath the tooth lined with smooth white dentine, indicating that before resorption was complete a new

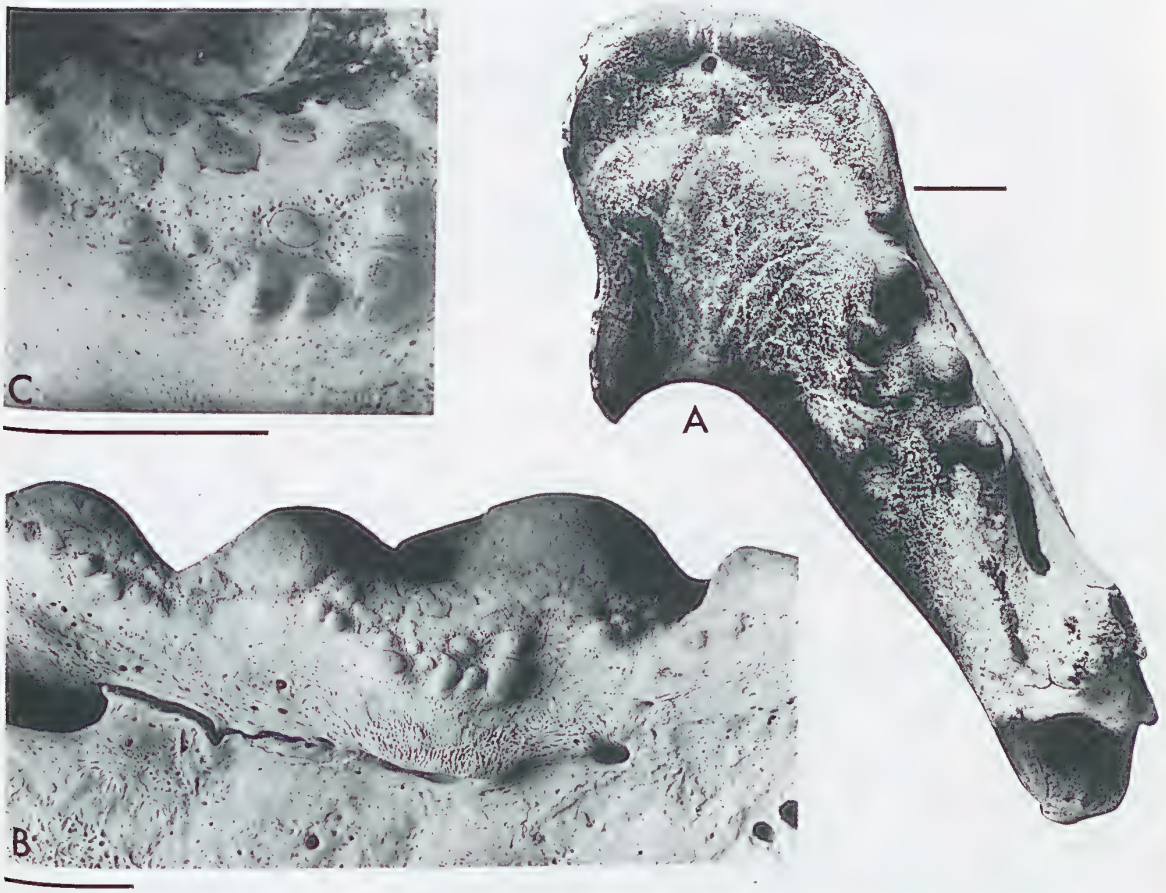

Fig. 7. **A:** (Scale = 10 mm) A larger mandible, P52565, at a stage of maximum development of the superficial dentine layer, with the sutures between the prearticulars, adsymphysial plate and dentary completely overgrown, and the simple dentine of the superficial layer almost completely invaded by dark pleromic dentine. Specimen without NH_4Cl coating. **B,C:** (Scales = 5 mm) Lateral views of same specimen showing marginal denticles fully grown, with worn tops, and partly overgrown by new bone. C, in particular, shows the ends of the dentine canals (dark coloured spots), the layer of enamel around the denticles (dark coloured rims) and the bone growing around the base of the denticles and in places almost covering them.

constructional phase began, and the superficial dentine braced the tooth sufficiently strongly for it to remain in position. The animal died during a subsequent resorption phase which had not advanced far enough to allow the tooth to fall free (Fig. 2A,B).

Behind the developing front, thin, steeply inclined columns of brownish pleromic dentine formed within the white layer. These columns of dentine have resulted from the pleromic infill of spaces that were not completely occupied during the formation of the white dentine sheet, or spaces that were resorbed subsequently. This process of pleromic infill must have preceeded apace, and a stage was reached when almost all the white dentine was replaced. At that stage, only small patches of bone appeared on the buccal surface surrounded by the mass of dark-coloured dentine. A fine example showing the complete sequence from unaltered bone to solid dentine is to be found on the posterior part of the right ramus of the mandible P52565. This is an example of the provision of a framework essential for pleromic dentine to develop as a consolidating tissue. If the only dentine in this region was that of the primary denticles, then it is most likely that pleromic growth of dentine developed from them. This type of extention of dentine has been illustrated previously (Smith, 1977: figs 14, 62, 63). Entire worn surfaces of pleromic dentine and bone feature strongly in the dentition of *Holodipterus* (Smith, 1977: fig. 60).

At the stage of complete dentine cover, the surfaces of the pterygoids and the prearticulars are irregularly pitted and coarsely rugose. The pitting results from wear of the softer white dentine patches, and the linear depressions marking the rugosities result from wear of elongate, irregular strips of white dentine. These are thought to have marked the margins of previous resorption phases prior to the addition of new superficial dentine layers. On specimen P50999 these strips cut obliquely across the median part of the palate, producing a pattern of irregular and graded subdivisions of the callosities which mimic a row of old tooth bases, though the resulting ridges are set at an angle to the three tooth-bearing ridges (Fig. 5A).

At its most extensive phase of development, the pleromic dentine on the mandible covers most of the prearticulars, the whole adsymphysial plate and the dorsal surface of the dentary (Fig. 7A). Over this entire region, the surface has the same irregularly pitted pattern, and shows a number of rugae that extend from deep in the lingual furrow across to the medial aspect of the tooth rows.

This dentine provided a hard-wearing surface which took on a high polish in some regions. It has every appearance of permanence, but it, too, was subject to extensive resorption and replacement. However, resorption was rarely if ever complete, as is apparent on the specimen illustrated in Figure 1. This individual shows extensive resorption, but the palatal callosity shows at least three stepped edges marking successive resorption phases. This observation leads to a discussion, in the following section, of the remaining features of the dentition – the dentine masses on the median region of the palate and the heels of the prearticulars.

Dentine Callosities

Dense masses of dark-coloured dentine, with irregular surfaces and outlines, occur on the median part of the palate and on the heel of each prearticular. They do not have enamel on their surfaces.

The larger palatal callosity is posteromedial and is present on all five specimens available to us. It is approximately equidimensional in some specimens, but has linear anterolateral extensions on others. Its margins are never sharply demarcated as formed surfaces, but show extensive resorbed embayments. Some specimens (P56045, CPC25739 and CPC25740) have a second callosity on the anteromedial part of the palate, but such a feature is lacking on others. It is approximately oval in outline but its margins also usually show signs of resorption. Presumably resorption was complete on some individuals.

The posteromedial callosities also show extensions of various lengths directed towards, but usually not precisely in line with, the first and second marginal teeth, giving the impression that long, radial tooth rows are present. If this were true, the radial ridges would represent extensively worn replacement growth of dentine beneath each tooth; however, the difference in tissue arrangement between this region and the most lingual tooth in each row makes this interpretation improbable. Also, in extensively resorbed individuals (Figs 1A,B; 2A,B), these ridges are shorter and denticles cover the surface of the palate between them and the adjacent teeth, so that they can be seen to be relicts of the formerly continuous dentine sheet, and not worn down enamel-covered teeth.

The problem of the growth of the callosities may be resolved as follows. Those specimens in which the surface layer of dentine has been most completely replaced by pleromic ingrowth have dense dark dentine all around the callosities. Those with a minimum of superficial and pleromic dentine on the palate overall have callosities surrounded first by a narrow, incomplete zone of partly replaced bone, and then a sheet of denticles. Presumably during the phase of maximum resorption, part of the pleromic dentine sheet adjacent to the callosity was not removed. During the next expansive phase the dentine in this zone was able to grow pleromically into the underlying bone. It would then have been even more difficult to remove during the next resorption phase, being either too thick to resorb and/or being raised above the resorptive tissue. Because resorption does not leave regular margins, the outlines of the callosities would be irregular, and

different between specimens or even on the two sides of the one specimen. Specimen P50999 illustrates this sequence very well (Fig. 5A,B). Successive resorption edges are clearly defined around both anterior and posterior edges of the posterior median callosity. In this way, starting from a small patch of unresorbed pleromic dentine around a number of denticles, each callosity increased in area and thickness.

Another factor to be considered is that the cells responsible for resorption would have been least effective in areas of maximum wear stress, and the dentine would have remained unresorbed in these areas. The median callosities which worked against food manipulated by the basihyal/basibranchial tooth plates, and the sub-radial ridges that directed food inwards from the marginal teeth, would have been areas of wear stress. This matter is discussed in more detail in the subsequent section on occlusion and wear.

Growth of Pterygoids

As is normal for members of the denticulate group, denticles cover the main part of the parasphenoid as well as the pterygoids, and the sutures between these bones are completely obscured. However, palates that can be viewed dorsally show the outlines of the parasphenoid very clearly; the posteromedian callosity lies across its anterior junction with the pterygoids. Because this callosity is present in all specimens available to us, including even the smallest ones, and because it never shows resorption in the mid-line, the pterygoids and parasphenoid have been able to grow areally only by addition to their free lateral and posterior margins (see Fig. 3C,D). This

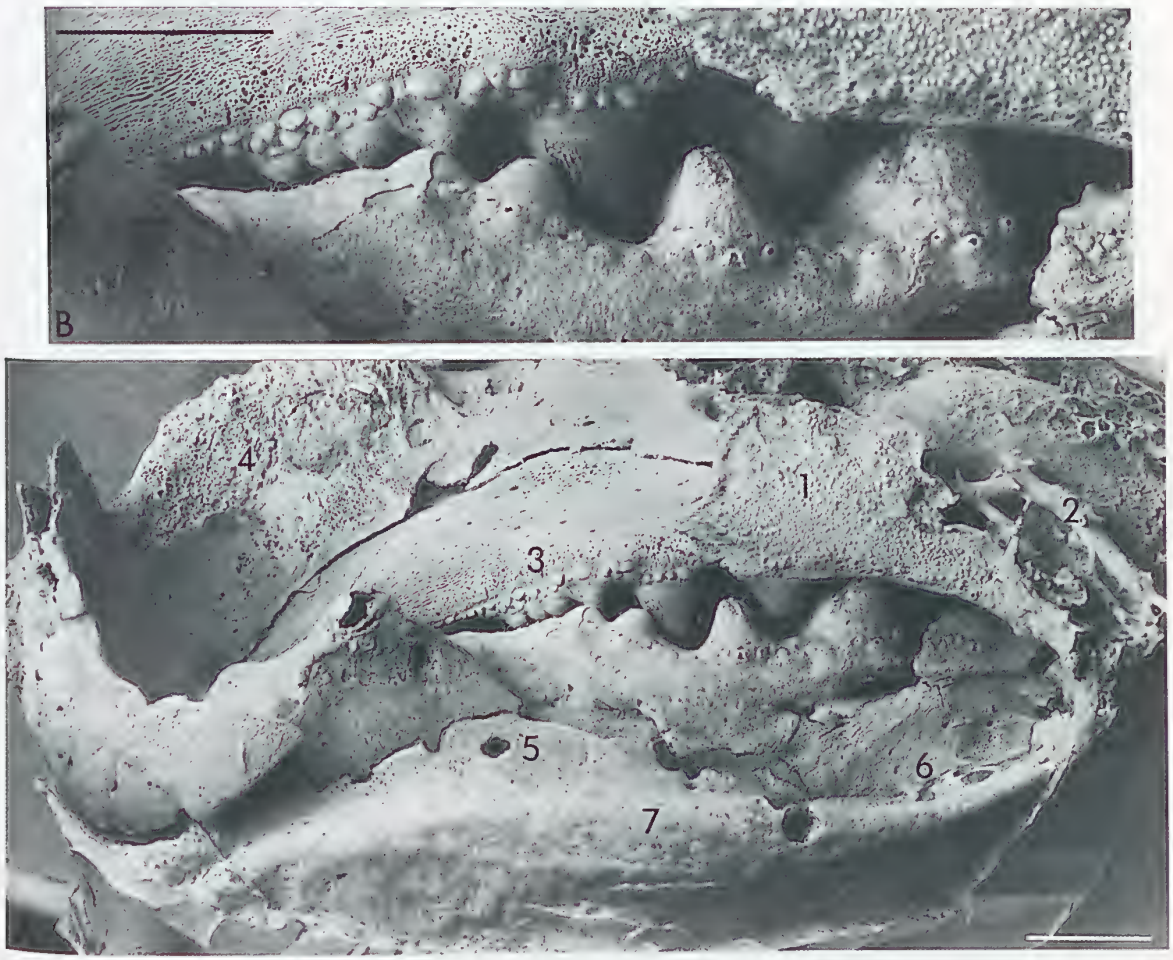

Fig. 8. (Scale = 5 mm) Lateral view of an eroded skull and mandible, P52568. The mandible had been largely lost by solution prior to collection, and the vacated bone space has been filled with PVC prior to laboratory etching. The marginal denticles on the prearticular have bubbles where the PVC did not completely fill the mould. **1**, cheek bones forming a deep arch; **2**, tubuli of the snout; **3**, pterygoid; **4**, side of braincase; **5**, upper edge of surangular; **6**, deep labial pit; **7**, upper edge of originally cosmine-covered part of external dermal bones.

point is well demonstrated also by the transverse palatal sections illustrated in Figure 19. We cannot demonstrate this for other denticulate genera but nevertheless it probably was the situation in all of them. However, we note that *Dipnorhynchus* and *Speonesydrion*, with their dentine-covered palates and posteromedian callosities, could not have added to their pterygoids in the mid-line, (see Campbell & Barwick, 1985). We believe that this was a character shared by all primitive dipnoans. It was soon lost in the lineage that developed crushing plates – e.g. *Dipterus, Scaumenacia* and *Chirodipterus* – in which the median suture opened and became a site of growth.

OCCLUSION, WEAR AND REMODELLING

Specimens P52568 (Fig. 8) and CPC25738 (Fig. 3D) show the occlusal relationships very clearly. As indicated previously, on P52568 the marginal teeth of the lower jaw lie outside the line of those of the upper jaw. Consequently, the second tooth on each row in the lower jaw occludes with the outer row in the upper jaw. The surface of the mandible drops away steeply on the lingual side of the second teeth and the palate is highly arched inside the second tooth in each row. Consequently, occlusion is restricted to the marginal rim of the palate.

These observations explain the presence of a

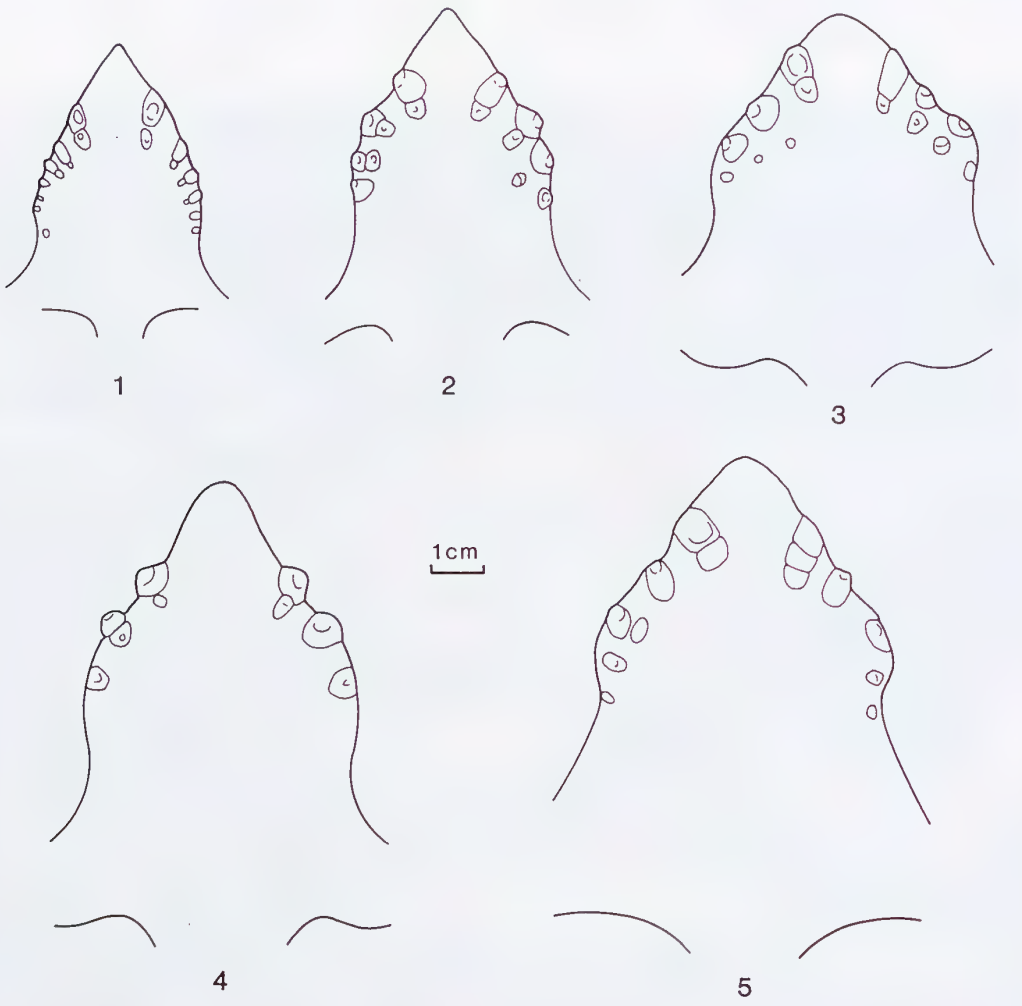

Fig. 9. Palate outlines of five specimens drawn at natural size showing the variation of palatal outline with the addition of new teeth at the ends of the rows. The large lateral lobes are produced by the addition of teeth at the ends of rows 2, 3 or 4 without corresponding additions to row 1. The anterior angle of the palate is clearly controlled by the addition of new teeth to row 1 and the rate of forward growth of the anterior ends of the pterygoids. 1 = CPC25740; 2 = CPC25738; 3 = P52569; 4 = P56045; 5 = P50999.

maximum of two teeth in the second and third rows on the palate. For occlusion to occur while the arch of the palate was maintained, the second tooth in each row of the lower jaw had to occlude while the outside (labial) one was being added; the inside (medial) one was out of occlusion and therefore it was shed. Those specimens that have only one tooth in the row died in a transition stage when an inner tooth had been lost just after the outer one had become functional.

Wear on the posteromedian callosity of the palate is always obvious, so much so that it often has a polished appearance. Specimen P50999, which has extensive dentine on the palate, also shows a great deal of polish on the areas adjacent to the callosity (Fig. 5A,B). Specimen P56045, which has most of the superficial dentine resorbed, has the crests of the adjacent denticles, particularly those behind the callosity, worn down to approximately the same level. These phenomena are to be explained as the result of abrasion by food moved by the basihyal/hypobranchial tooth plates against this part of the palate.

A model for control of resorption and regrowth, based on electrophysical theories of balanced bone growth and resorption, could be considered as applicable to the changing morphology of *Holodipterus*. This proposes that cyclic growth is a result of negative feedback in the oral system (Bassett, 1971). The theory relies on the observed phenomena of bone loss on the endosteal surface together with bone deposition on the corresponding periosteal surface, with the result that the bone in that region changes position or shape. Experiments have elucidated several phenomena that can explain this selective differential activity on opposing bone surfaces. One is that application of a cantilever force to a bone will cause a potential difference to occur at the two bone surfaces, a negative one at the concave surface and a positive one at the convex surface. The second is that, in response to extrinsic negative charge, osteoblasts become active and put down bone at an increased rate; in response to positive charge, osteoclasts remove bone at that surface in excess of any later deposition. The explanation of how the charge is generated is generally accepted as a piezzo electric effect in the crystals of the bone tissue; this effect results from the bending of either the hydroxyapatite or the collagen protein crystals. It must be assumed that this can also happen in the bone tissue of *Holodipterus, in vivo,* thus producing different phenotypes as a result of epigenetic control through tensional forces.

CYCLIC DEVELOPMENT

It will be obvious from the above account that the buccal dentition in *H. gogoensis* grew by a series of cycles involving massive resorption and redeposition of tissues. We have no knowledge of how many cycles were involved in a single life history. Judging from the size and spacing of the teeth, and assuming that growth has involved the loss of a tooth in each successive cycle, the number is unlikely to be less than six or more than ten.

Arbitrarily taking the onset of a cycle to begin with the initiation of bone growth to support a new generation of marginal teeth on the mandible, we recognise the following phases.

(i) New bone was laid down along the mandibular symphysis while remodelling of bone elsewhere took place by resorption and deposition, and lobes of bone began to form on the prearticular margins at the sites where new teeth were to form.

(ii) New teeth were formed at each of the above sites on both prearticulars at approximately the same time; concurrently, denticles continued to grow and to be replaced over most of the exposed bone of the buccal surface, and the dentine in the callosities grew into the underlying and surrounding bone.

(iii) On completion of tooth growth, the superficial layer of dentine began to grow outwards to envelop both denticles and tooth bases; denticles continued to be shed and to be replaced in an irregular fashion in advance of the dentine sheet; new marginal denticles appeared on the outer vertical faces of the prearticulars below the level of the teeth.

(iv) Pleromic dentine gradually replaced much of the superficial bone layer as wear on the teeth and callosities proceeded.

(v) Resorption began at the margins of the superficial layer but also in patches within the boundaries of the layer; occasionally the base of a tooth was resorbed and it dropped off; behind the advancing resorption fronts new fine-textured bone grew over the stripped surface, and on this bone new denticles began to develop, reach maturity and then shed.

(vi) This process proceeded in all the regions taken out of the functional biting surface by upward growth of teeth and callosities, until all the dentine except that in one or two marginal teeth in each row, and that in the callosities and their immediate environs, had been removed. The cycle was then completed.

A similar cycle would have operated on the palate, but because teeth were added alternately in the upper and lower jaws there must have been a 180° phase difference. As tooth growth was completed and the superficial dentine layer began to expand in the mandible, resorption would have been nearing completion, and new bone growth for the initiation of new teeth on the pterygoids would have been about to begin.

This may seem to be an improbable scenario, but it is susceptible to testing because, as we have shown, specimens P52568 and CPC25738, have the opposing jaws in position. In P52568 the mandible had reached the stage where the marginal teeth had been added and new denticles had begun to appear on the outer face of the prearticulars, though the

addition of bone and denticles of the development stage had not been completed (Fig. 8). It was probably in the late stage (iii) of the above sequence when it died. The denticles on the lateral face of the pterygoid, on the other hand, are somewhat worn and in several places their bases were being overgrown by new bone. In the vicinity of the tooth bases they had been partly engulfed by superficial white dentine. In one place there is a small outgrowth of new bone capped by a new enamel-coated denticle. The pterygoids must have been just entering a new phase of lateral growth prior to the initiation of a new series of marginal teeth. The surface of the palate has a continuous sheet of denticles across the part posterior to the median callosity. In front of that the superficial sheet of white dentine was extensive, extending around the bases of the remaining teeth. A couple of small circular patches and a rather larger anteromedian patch of denticles occupy areas from which the dentine sheet had been recently resorbed. The posterior edge of the main sheet also shows resorption. In this respect too, the palate shows the initiation of a new growth phase. Both lateral and ventral palatal surfaces suggest that it had begun stage (v). The specimen therefore clearly corroborates the hypothesis.

Specimen CPC25738 (Fig. 3D) has the palate and mandible precisely articulated, and the most lateral teeth on the prearticulars lie outside the line of the most lateral teeth on the pterygoids. The prearticular teeth had obviously just been added because they overhang the underlying bone and are almost unworn. No marginal denticles are present. The marginal teeth on the pterygoids are supported by their underlying bone, and show a few marginal denticles some of which are worn. A new row of pterygoidal teeth was about to be added when the animal died.

HISTOLOGY

In view of the many unusual morphological features of the dentition, including the extensive changes produced episodically by massive phases of resorption, it has become essential to reconsider previous interpretations of the histology of the tissues and, where possible, their histogenesis and growth. In particular we regard information on the marginal teeth, the superficial dentine layer, the callosities, and the relative position of the denticles, as crucial to a decision on the relationships of *Holodipterus*. Apart from those at the margins of radiate 'tooth plates' (for example in *Speonesydrion)* isolated large teeth have been described only in *Fleurantia* and *Holodipterus,* both of which were considered to be members of the denticulate group by Denison (1974), Miles (1977) and Campbell & Barwick (1983). *Uronemus* has recently been placed in the group with tooth plates (Smith, Smithson & Campbell, 1986).

The histology of the teeth has always been problematical since originally the only available vertical section of a tooth was affected by preparation artefacts (Fig. 10D; Smith, 1977), and it comes from the posterior end of a prearticular plate where teeth are rather poorly developed. However, three new vertical sections through a marginal tooth of the anterior ridge on a pterygoid have now been prepared from specimen CPC25738. In addition, the adjacent block-face has been prepared for S.E.M. by polishing and etching with 1 normal HCl for 1 minute. As a result, completely new information is available, including the relative hardness of the tissues, and this, together with re-examination of the original section (P52569), has enabled us to modify our previous understanding.

The histology of five structures will be described: the teeth, dentine callosities, superficial dentine layers, and both marginal and superficial denticles.

Marginal Teeth

The original section and the new ones are illustrated in Figures 10–18. They show a worn tooth tip and, in the new sections, a distinctive basal margin on the labial side of the tooth. This is formed of pallial dentine covered with enamel (Figs 10–11). In all sections, larger spaces between the dentine and the bone are present in the centre of the tooth, and this is presumed to be a region where continued growth of the central dentine could occur (Fig. 10A–D). The tissue at the centre of the tooth tip is very compact and relatively homogeneous, the pulp canals being much narrower than those at the base (Figs 10A–C; 15A). This tissue beneath the worn tip shows little distinction between regions of interstitial and circumpulpal dentine. More basally the two tissues can be readily distinguished, particularly at the margins (Figs 11A, 12A) and where the tissue joins the bone. These three regions, and the arrangement of the pulp canals are shown in Figure 13. All of the compact dentine (but not the interstitial or pallial dentine) has a cross-hatched appearance in polarised light (Fig. 10B) similar to that of petrodentine (Smith, 1984: fig. 28); in particular it is similar to the petrodentine of *Chirodipterus* (Smith & Campbell, 1987: fig. 35). However, there appear to be differences between the two genera in several details. In *Holodipterus* only short channels for cell processes (Fig. 12B) can be seen at the formative surfaces which are continuous over fairly wide areas within the extensive system of pulp canals. Many extremely delicate tubules can be seen throughout this region of developing dentine prior to the formation of any circumpulpal dentine (Fig. 12B). A region with fine branching tubules, most of which are wider immediately adjacent to the pulp canal, is illustrated in Figure 14. The interpretation of this region in Figure 13B shows the wide tubules in the circumpulpal dentine branching into finer ones in the main dentine mass. It is not unusual in extant forms

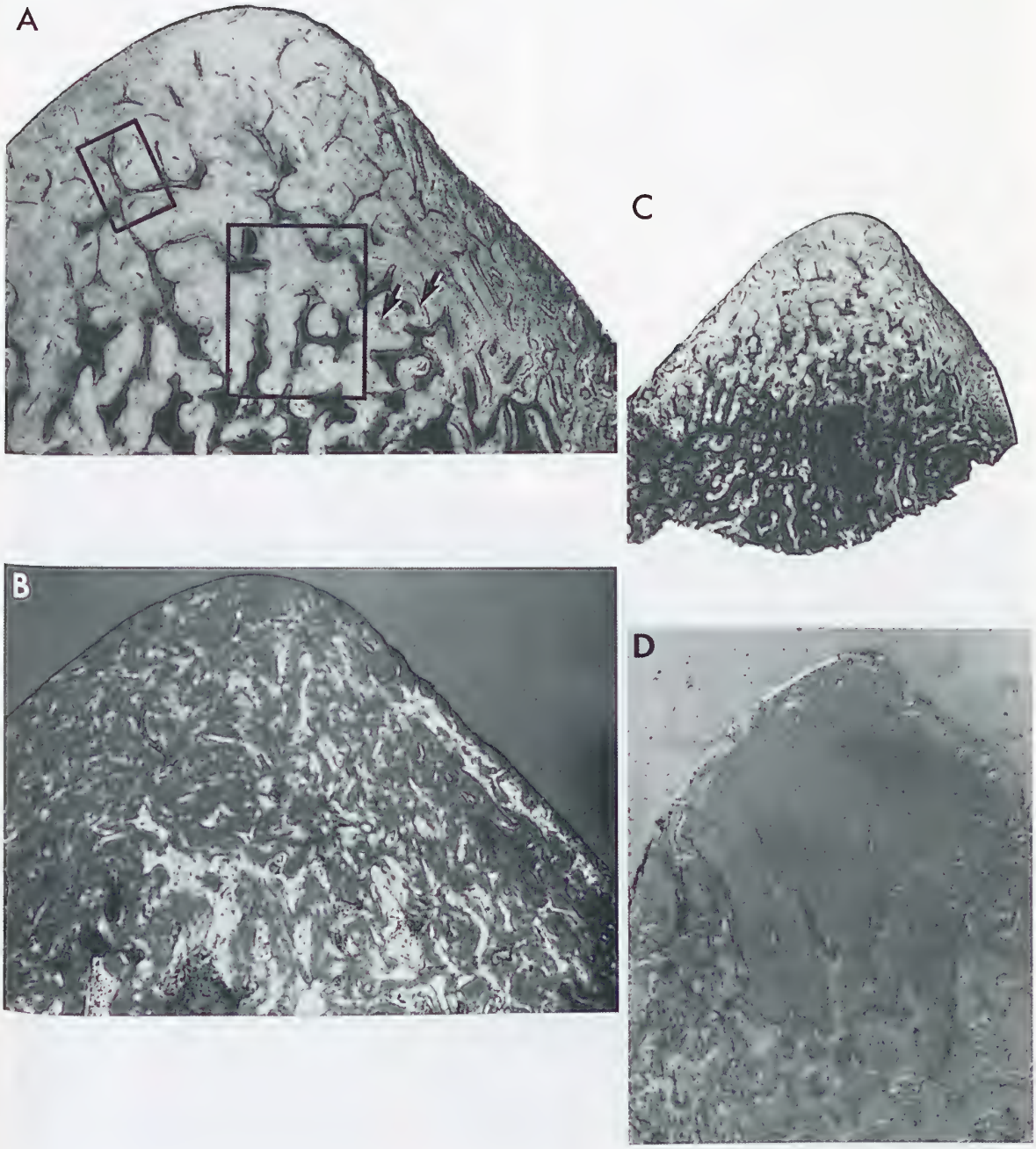

Fig. 10. **A,B:** (x 40) The worn tooth tip is compact dentine above trabecular dentine at the base. Enamel covers a thin layer of pallial dentine on the right at the basal labial margin. The dentine at the tip is relatively translucent (A) and contains very narrow, branching pulp canals. These lead into wider canals in the basal dentine which join with the medullary spaces of the bone. Within the basal dentine, in contrast with that of the tip, small patches of interstitial dentine remain (arrows). In polarized light (B) the canals filled with calcite are strongly birefringent, the dentine shows regions of weaker birefringence, with bands of opposite sign in a woven pattern. **C:** (x 16) The whole tooth section; two other sections were cut either side of this and the remaining block face prepared for the S.E.M. **D:** (P52569, as in Smith, 1977: fig. 57) (x 40) shows the poor preservation of tissues in this specimen relative to the new sections, but emphasises the region of compact dentine at the centre.

[The photomicrographs and the S.E.M.'s in Figs 10–18 are from vertical sections cut in a labio-lingual plane through the marginal tooth on the anterior row of the pterygoid (CPC 25738).]

to find some delicate tubules within the petrodentine, but usually these are not extensive and they run only a short distance into the petrodentine. The distinctive features of the tooth of *Holodipterus* are the very irregular arrangement of pulp canals (Fig. 10A) forming a network through the tooth, and numerous fine branching tubules extending from them. The compact dentine seems to have formed initially by adding layers onto the smooth lamellar tissues forming trabeculae (which are assumed to have been dentine), and subsequently directly on to itself. These trabeculae were at first rather porous as they were readily impregnated with dark-stained calcite during diagenesis (Figs 10A; 11A,B). In the tooth tip it is difficult to distinguish these trabeculae. Continuous growth lines are not seen across the tooth as in the tooth plates of *Chirodipterus* (Smith & Campbell, 1987: figs 65, 66).

A parallel surface immediately adjacent to the one from which the histological section was cut, and which shows all the same tissue regions, has been prepared as a polished-etched surface and examined in the S.E.M. (Figs 15–18). The tissue complex of the tooth tip (Figs 15; 16A,B) is very compact hard dentine, the bulk of which has an apparently random arrangement of woven, crystal-fibre bundles with very small spaces of narrow diameter between them (Fig. 15D). These may be the fine tubules seen in thin section in Figure 14. The pulp canals in this region are lined with two distinct layers. The first is formed of tissue similar to that making up the main dentine mass of this region; the second is a more homogeneous and relatively narrower lining to the pulp canal itself (Fig. 15B,C). This double layering is also seen in the optically examined thin sections in which a translucent layer of circumpulpal dentine lines the canal (Fig. 12A), and a thin layer of tissue that is possibly diagenetically altered, lies adjacent to this.

In the tooth tip, the zones of dentine surrounding adjacent pulp canals are juxtaposed leaving isolated irregular interstitial regions (Fig. 13). These regions

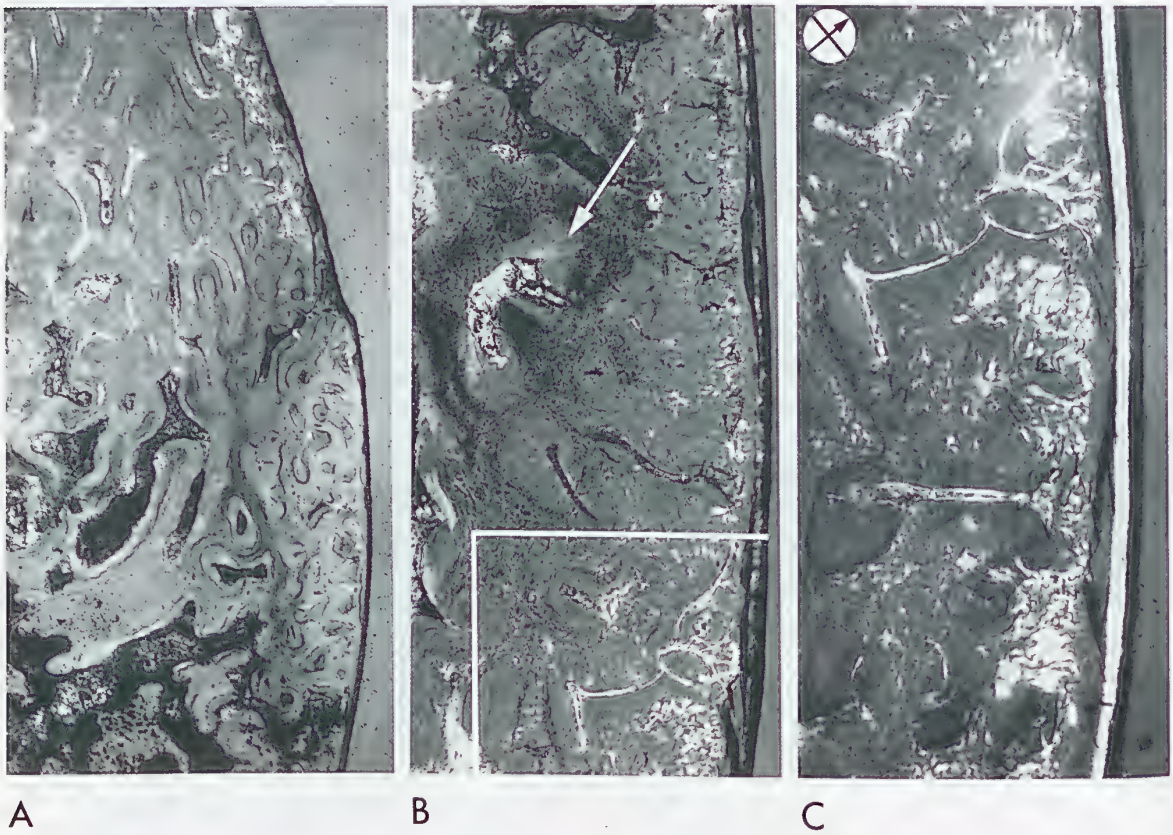

Fig. 11. Basal lateral margin of the tooth in Fig. 10C to show the structure of pallial dentine, the basal dentine and the enamel layer. **A:** (x 64) Extensive pulp spaces between the bone and immature basal dentine lead into narrower canals within the compact dentine, mostly lined with dark calcite. Regions of circumpulpal dentine are distinct from the interstitial regions; the latter show a diffuse black stain (arrow, Fig. 10B). **B:** (x 160), **C:** (x 250) A magnified and extended area of the box in B. The pallial dentine contains fine terminal branches of the narrow pulp canals, radial to the tooth surface and ending below the enamel dentine junction. Strong birefringence of the enamel layer in C shown between crossed polars (direction of polarizer and analyser as shown).

are defined in S.E.M.'s by changes in the direction of the crystal fibre bundles (Fig. 16A,B). In contrast, the regions towards the tooth base (Figs 16C,D; 17) have the junctions between adjacent dentine zones marked by progressively wider spaces that are occupied by the smooth homogeneous tissue mentioned above, in which no crystals have been observed (Fig. 17C,D). The wide open canal spaces are clearly seen in this region (Figs 16C,D; 17A–C), and they are interpreted as forming-surfaces of this type of compact, hard dentine with many very small open spaces between the crystal groups. The pulp canals are not, at this stage, lined with further dentine, and the youngest region of this compact dentine is very open, the canals being permeated in many regions by calcite crystals (Fig. 17C). The junction between the forming compact dentine and the dentine trabeculae shows little continuity of structure across the boundary (Fig. 17D). This would be consistent with a different tissue type forming from this boundary onto an initial framework of less mineralised trabeculae of dentine. These features (viz. the hard dentine deposited on to soft trabeculae) make the type of dentine in the *Holodipterus* tooth different in its mode of growth and arrangement from petrodentine. However, in its hardness and microstructure it is very similar to petrodentine. At the margins of the tooth (Figs 15A; 18A,B) the extensive development of this hard dentine has left limited areas of pallial dentine beneath the enamel layer. Here, also, regions of smooth homogeneous tissue (dentine trabeculae) remain within the harder dentine (Fig. 18B).

In summary, the interpretation of this extensive hard compact dentine is problematic. The best that can be said at present is that it is clearly a form of hypermineralised dentine, but its mode of growth is different from the hypermineralised dentine found in any dental plates. In some respects it is like an

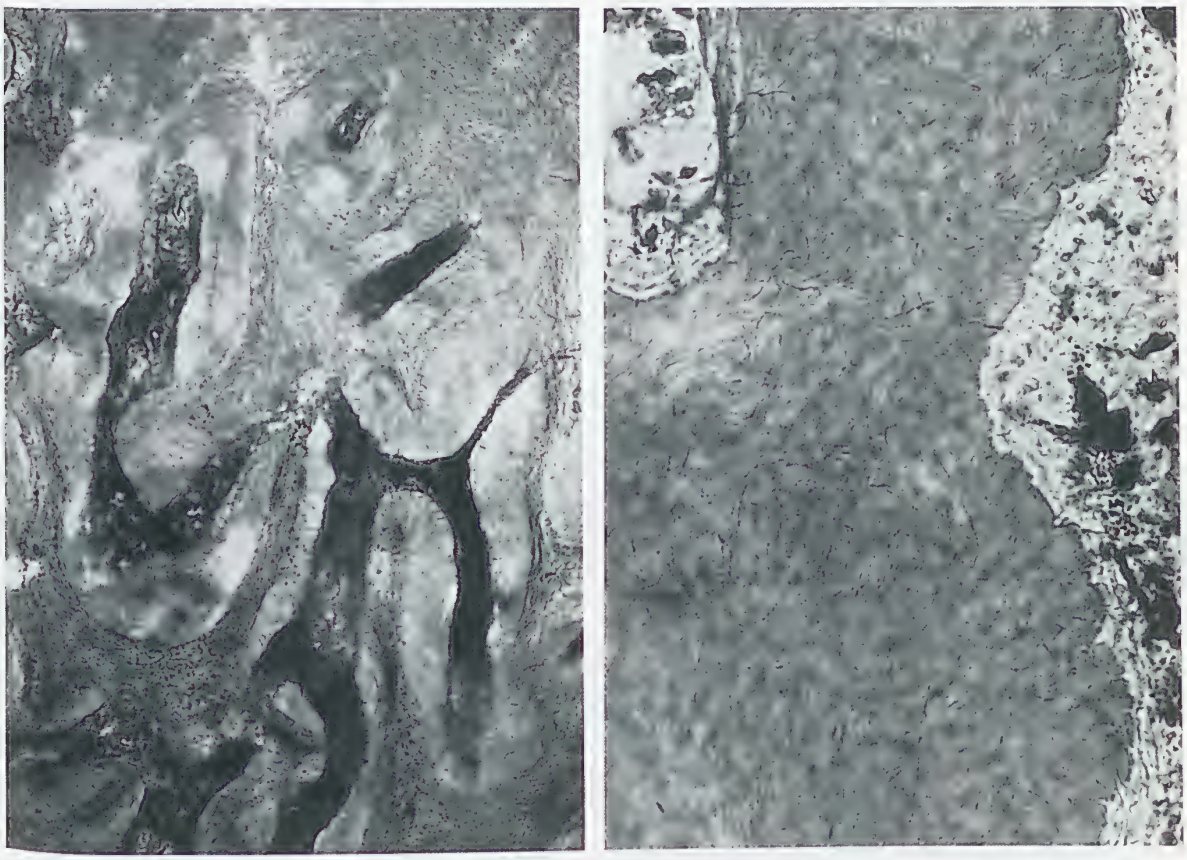

Fig. 12. **A:** (x 180) Dentine at the base of the tooth. A clear difference can be seen between interstitial and circumpulpal regions of dentine. The wide pulp canals in the formative zone at the bottom of the illustration have relatively narrow regions of circumpulpal dentine and the interstitial dentine has a diffuse black stain. **B:** (x 450) One region from the centre of the tooth where there are forming surfaces of dentine in which short wide tubules lead into extremely fine tubules branching and coursing throughout the dentine. No zone of circumpulpal dentine exists and the pulp canal is relatively wide.

intermediate between pleromic dentine and petrodentine, the two being used together to make the composite hard tissue. This difference may be related to the fact that in *Holodipterus* the teeth have only limited periods of growth before thay are shed, whereas in normal tooth plates growth is continuous throughout life.

One region at the base of the tooth on the lingual side, suggests that the tissue between adjacent teeth on the radiate ridges forms from growth of the compact hard dentine onto the bone surfaces (Fig. 20). This is a continuation of the hard dentine of the tooth and is similar to the tissues of the callosities, described in the next section.

Dentine Callosities

Vertical sections through the posteromedial callosities, which appear superficially to be made of shiny black dentine, show a translucent, compact tissue closely intermingled with the bone (Fig. 21A–D). The extent of this tissue relative to the parasphenoid bone is clearly seen in Figure 19A & B. The pulp canals are narrow and surrounded by circumpulpal dentine through which short irregular tubules run from the pulp canals. The dentine between the pulp canals is translucent, homogeneous, and exhibits a pattern of birefringence in which alternating crystal bundles have opposite signs; these are features of petrodentine and pleromic dentine as found at the margins of the tooth plate in *Chirodipterus* (Smith & Campbell, 1987).

In restricted regions, a free surface between the bone and the dentine can be observed, and from this surface the dentine grew. Immediately above this there are strong growth lines within the dentine, following the contours of the forming surface below (Fig. 21D). This is a feature of intermittent dentine growth following creation of a resorption space within the bone, similar to that shown by petrodentine growth in *Chirodipterus*. Similarly, outgrowths of dentine occur as pocules (i.e. small cup-shaped bodies) occupying spaces in the adjacent bone. This has been previously illustrated by Smith

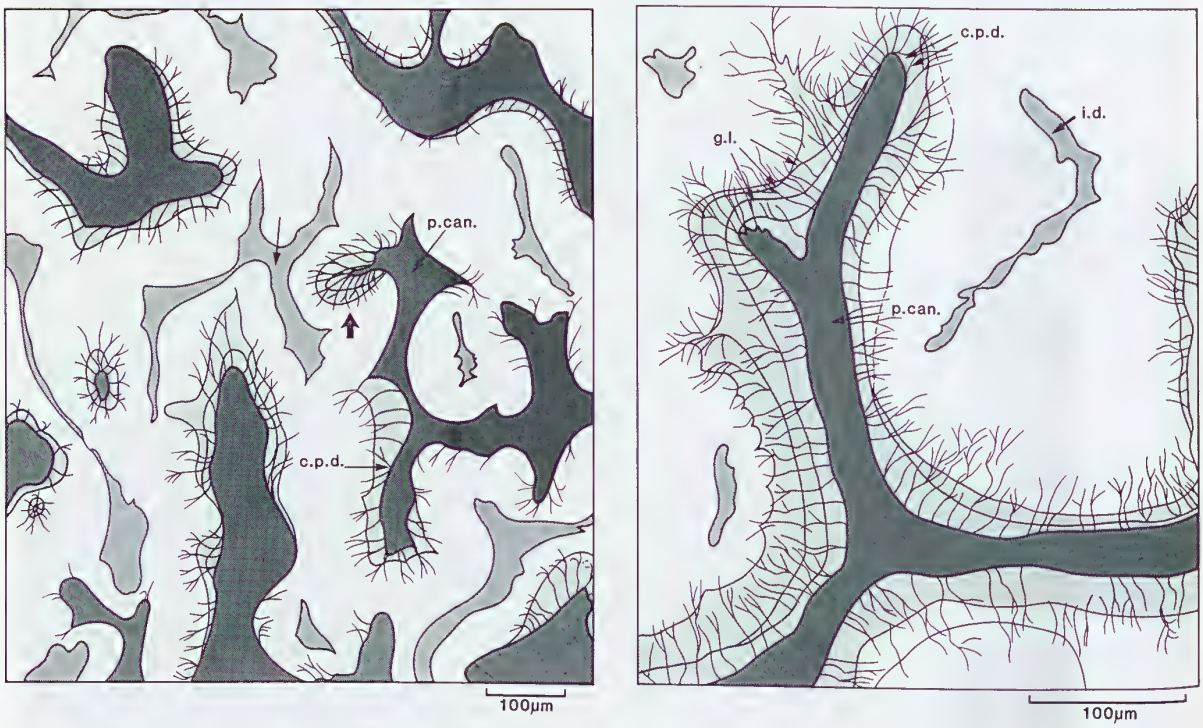

Fig. 13. (Scale bars = 100µ). **A:** Drawing of the central dentine beneath the tooth tip and towards the basal tissue, to show the arrangement of the different regions of dentine and separate growth zones around the pulp canals (p. can.). Smaller branches of the pulp canals are surrounded by several concentric layers of circumpulpal dentine (c.p.d., arrow) through which run irregular tubules. The mass of tissue between the pulp canals is hard compact dentine, but centrally amongst this are several islands of interstitial dentine (i.d.). The larger pulp canals towards the bottom are only partly lined by circumpulpal dentine. **B:** Drawing of the end of one pulp canal immediately beneath the tip of the tooth. This shows the same three regions of dentine as in Fig. 10A, but thick layers of circumpulpal dentine (c.p.d.) have narrowed the lumen of the canal and several growth lines (g.l.) can be seen. Numerous tubules run through these layers of dentine formed by addition to the surface of the compact hard dentine; the latter is generally without tubules, except the fine terminations of the wide tubules in the circumpulpal dentine, as shown in 14A and B.

(1977: fig. 14), where it was referred to as pleromic dentine.

Occasionally a bone surface can be seen covered only with vestiges of this hard dentine (Fig. 21A–C), most of which has been completely worn away. Nowhere is there any covering of enamel, but some surfaces are completely covered by denticles (Fig. 21A), or by the superficial dentine (Figs 21D; 22C). The most remarkable feature is that these denticles and the superficial dentine lie on a resorption surface where a reversal line marks the extent of resorptive activity in a phase where even this hard translucent dentine was removed from the surface downwards. After these phases of resorption the subsequent repair tissue is a single layer of denticles (Fig. 22A, B), or superimposed layers of denticles (Fig. 23B, D), or a very simple dentine layer (Fig. 22C). These may grow over old bone or partially resorbed pleromic dentine. Also, in some places a layer of finely trabeculate new bone formed over the resorption surface in conjunction with the formation of the denticles.

Superficial Dentine Layer

This is the white material observed on many surfaces and found surrounding the denticles, covering the bone surface and also enveloping the bases of the marginal teeth. It is exceedingly thin in many areas on both the pterygoids and prearticulars (Fig. 22C). Its histology is that of a very poorly developed, primitive type of dentine. This kind of tissue can occur anywhere in a subepithelial position, but is normally formed beneath an enamel layer.

In specimens preserved at the end of a depositional phase, considerable wear has occurred and the white tissue surrounding the tooth has been worn away to expose pleromic dentine that formed within this tissue as it was worn down.

Superficial Denticles

These are considerably smaller than the marginal denticles and have a simple structure as in

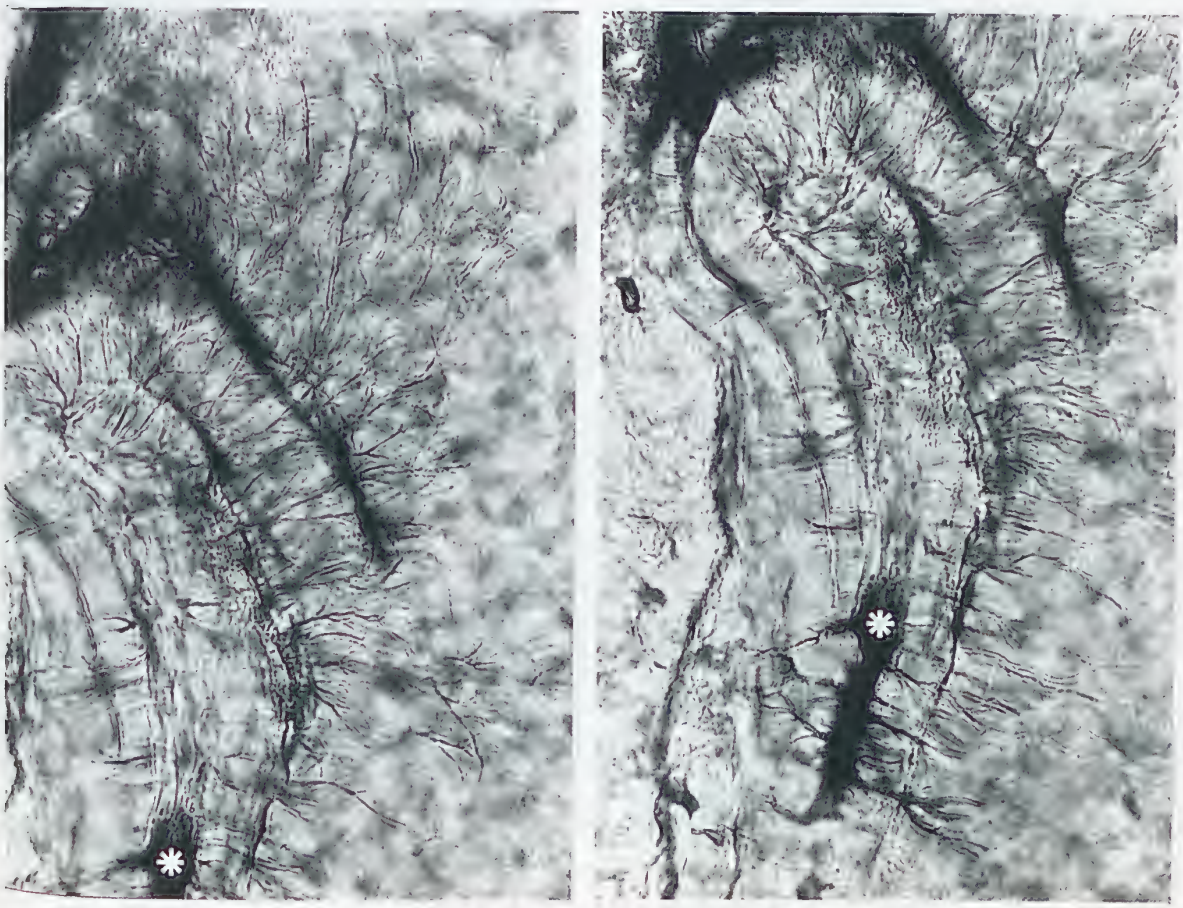

Fig. 14. (x 720) Two levels of a through-focus series, approx. 2μ apart, to show the same region of circumpulpal dentine around a narrow pulp canal (asterisk). The wide tubule spaces open into the pulp canal and lead into progressively finer and more branched tubules within the dentine. The lines parallel to the pulp canal surface, crossing the tubules at right angles, are assumed to be junctions between successive growth layers, i.e. growth lines. The asterisk is in the same position on the two photographs.

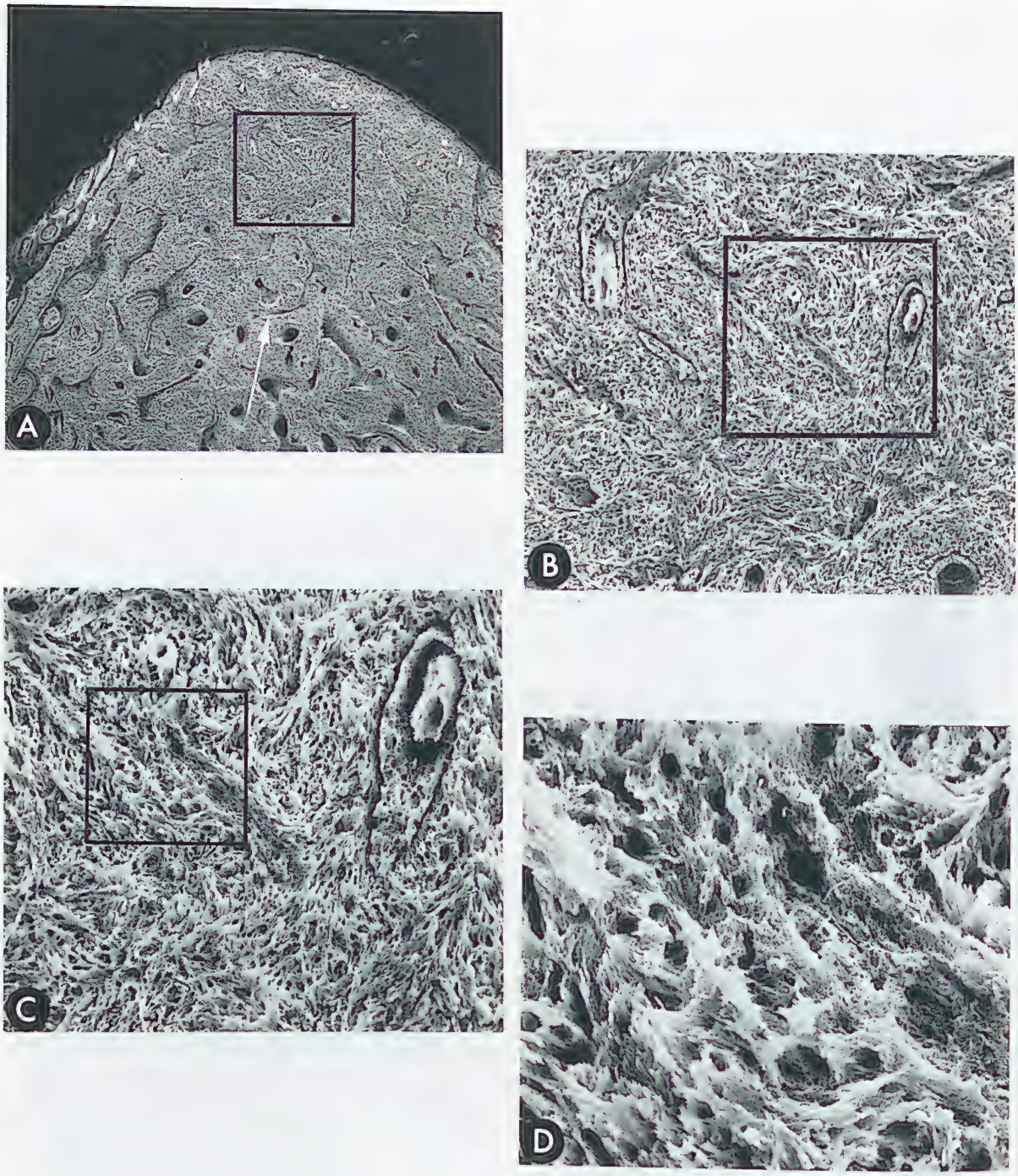

Fig. 15. **A:** field width = 2.7 mm. Field of the mature tissue, compact dentine at the tooth tip. Immediately beneath the worn surface the canals are infilled with biological apatite; towards the base the canal spaces are shown by the removal of the infilling sediment. (Rectangles show fields of B–C; arrow, field of Fig. 16A). Field widths: **B** = 0.6 mm, **C** = 0.27 mm, **D** = 90μ (0.09 mm). Fields from the region of the asterisk in A at increasing magnification show at least one layer of dentine concentric with each pulp canal. Groups of parallel crystals lie in several different planes within the compact hard dentine and are permeated by many small canals. Figs 15–18: CPC25738: see Fig. 10.

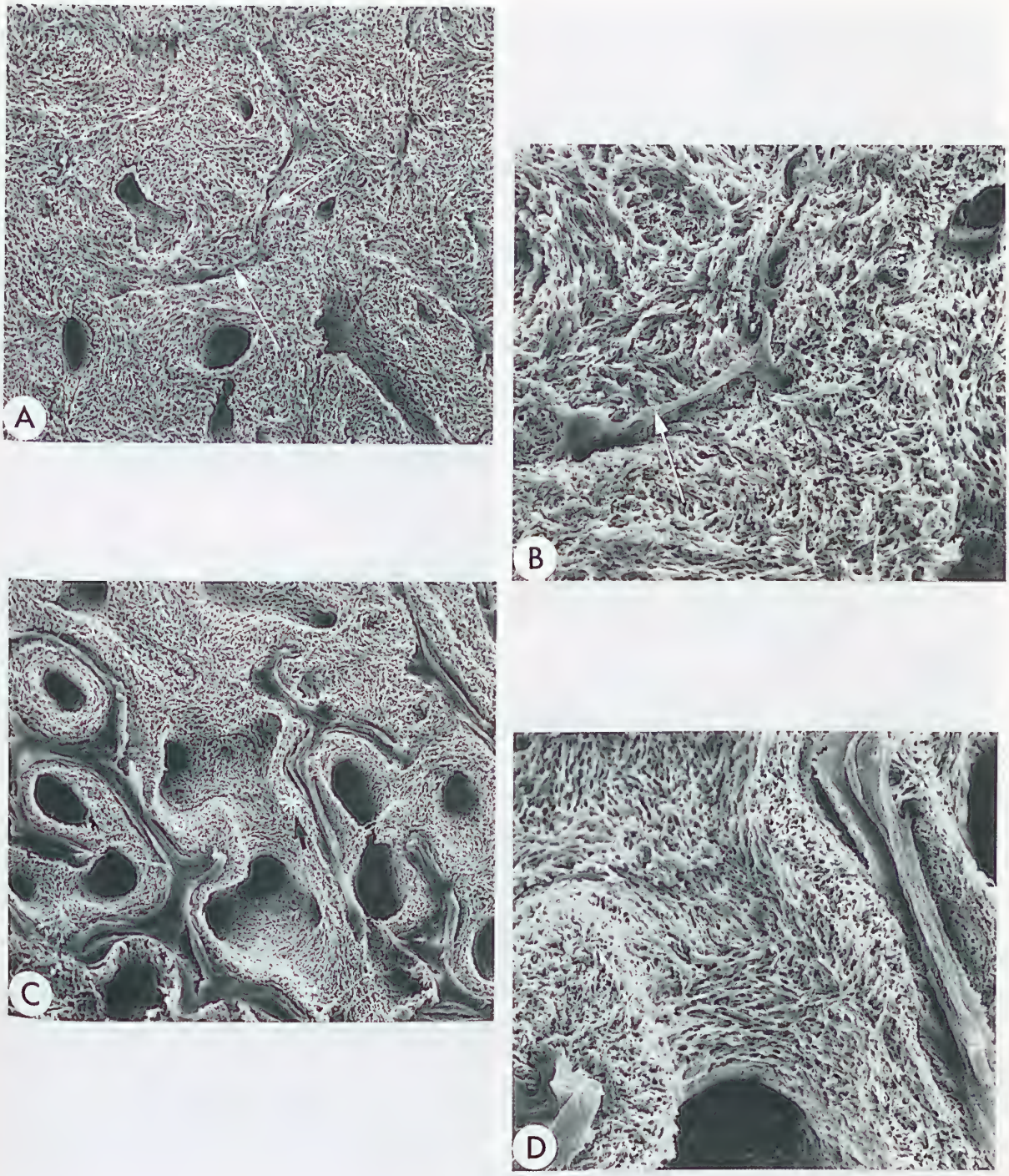

Fig. 16. Field widths: **A** = 0.9 mm, **B** = 0.27 mm. Zones of compact hard dentine are separated by narrow strands of smoother and more homogeneous interstitial tissue (arrows). The region is central to the tooth, immediately below the tip (arrow Fig. 15A). **C**, field width = 0.9 mm and **D**, field width = 0.27 mm. A region lateral and basal to that of A & B, both at comparable magnifications, with longer wider zones of interstitial tissue and wide, open canals with forming surfaces of compact hard dentine, but no infilling, concentric zones. (Field D, from asterisk in C.)

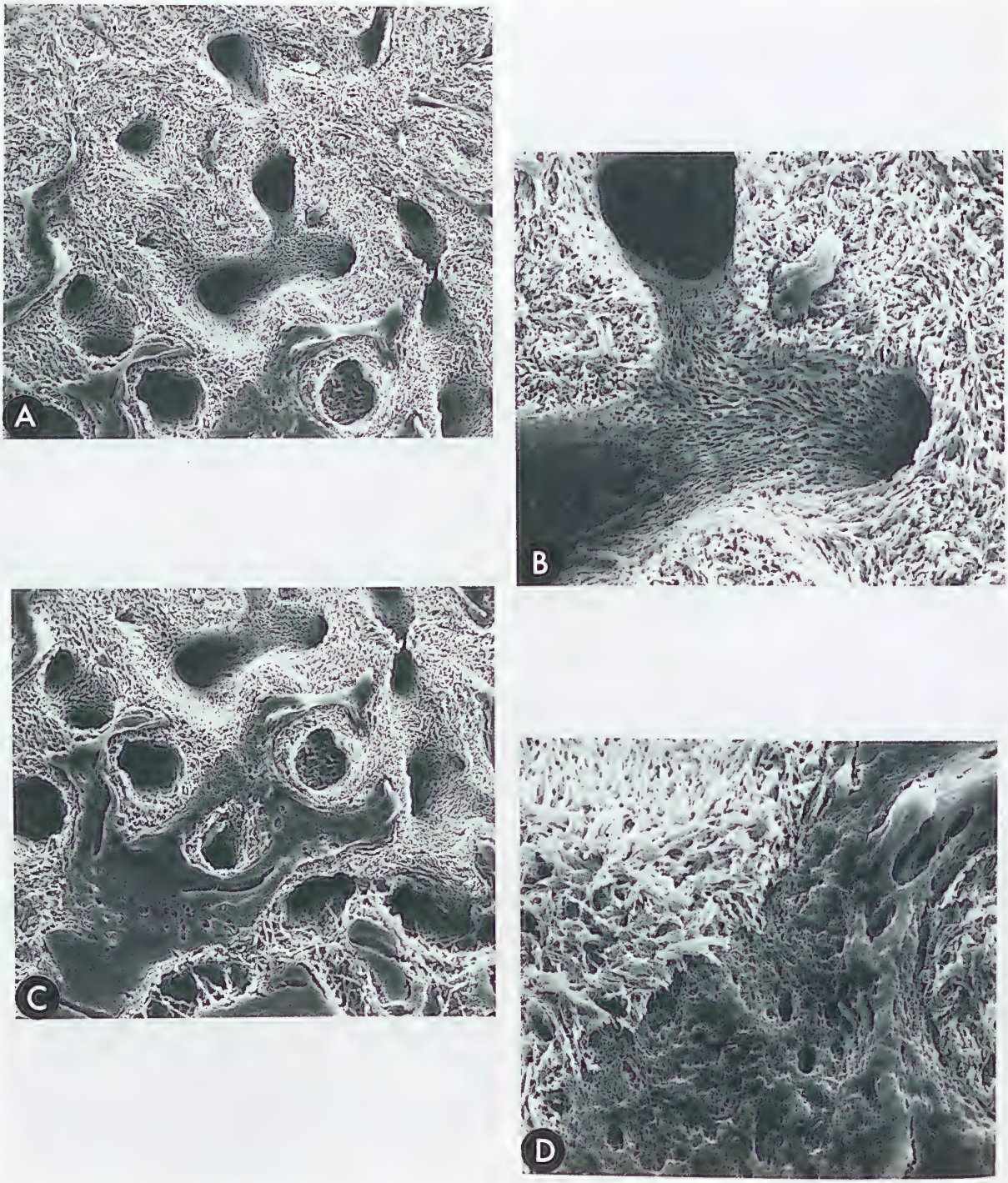

Fig. 17. Field widths: **A** = 0.9 mm, **B** = 0.27 mm. Region of basal central dentine with extremely thin interstitial regions and narrow zones of compact hard dentine around wide canals which show forming surfaces of this dentine in B. **C** field width = 0.9 mm, **D** = 0.18 mm. More basal than region A & B with very wide interstitial zones of smooth, homogeneous tissue and thin layers of compact hard dentine. The wide canal spaces are occupied by the remnants of etched calcite crystals. The junction between the compact hard dentine and the interstitial dentine is irregular, as is well shown in D.

Griphognathus, as was shown by Smith (1977: figs 34, 35). Beneath a thick layer of enamel there are many short, branched pulp canals from which tubules radiate into the pallial dentine; frequently the denticles have many accessory crests, each with a pulp canal (Fig. 22A). Superpositional growth of denticles occurred in many regions (Fig. 23B,D) but the denticle layer always formed on top of a resorbed surface of bone or dentine, demarcated by a reversal line and an interruption of the structure of the bone trabeculae (Fig. 23C). Many of these denticles became worn and served as a protective cover to the relatively delicate trabecular bone forming most of the palate (Fig. 22B). They may also have initiated pleromic growth of dentine on this surface. However, quite a few were removed through resorption of small patches, and therefore had a temporary role in formation of the dental surface.

Marginal Denticles

Marginal denticles are substantial structures relative to the denticles covering the palate and lingual surfaces. They formed tightly packed groups on the vertical margins of the pterygoids and prearticulars (Fig. 24A). It is notable that their histology is different from the scattered buccal denticles in that, beneath a very thin layer of pallial dentine, trabeculae of dentine form a robust framework for the circumpulpal dentine, leaving a system of interconnecting pulp canals linking up with the bone spaces (Fig. 24B,C). The cells that produced the dentine have left many irregular tubules with finer branches within the circumpulpal and trabecular dentine; these all link with the pulp canals.

The marginal denticles are of a type that could be regarded as semi-permanent structures that may have provided centres from which pleromic dentine could grow into the bone and later become associated with the worn tissues at the base of the teeth. Judging from the position in which they had formed, it is quite possible that they could have developed from the epithelium of an invaginated epithelial cuff at the margins of the prearticular and pterygoid dental plates. Though it is not possible to refute this or substantiate it by observations on these specimens, the position of the newest denticles at a distance deep to the lateral surface makes a subsurface position for their development more probable than a superficial one. In this, as in many other respects, they are unlike the marginal blisters in *Chirodipterus* (Smith & Campbell, 1986), though these too remain intact until worn or ingrown by pleromic dentine. Sections through a worn region of these marginal denticles show, in fact, that pleromic dentine had formed within the bone and contributed to the worn surfaces of the troughs between the teeth.

DISCUSSION

Review of Dental Form

Previous evaluations of the position of *Holodipterus* in a scheme of relationships have placed this genus within the group that lacks tooth plates (Denison, 1974; Miles, 1977; Campbell & Barwick,

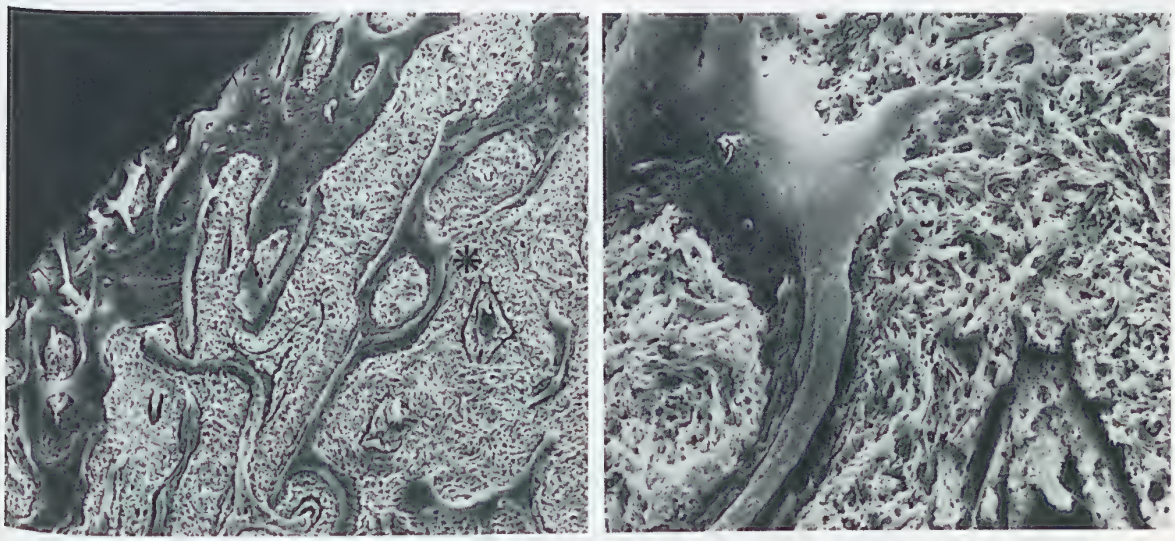

Fig. 18. Field widths: **A** = 0.9 mm, **B** = 0.18 mm. Regions at the lateral basal margin of the tooth to show extensive regions of smooth, homogeneous tissue of the pallial dentine continuous in places with the interstitial material (B, from the region asterisked in A).

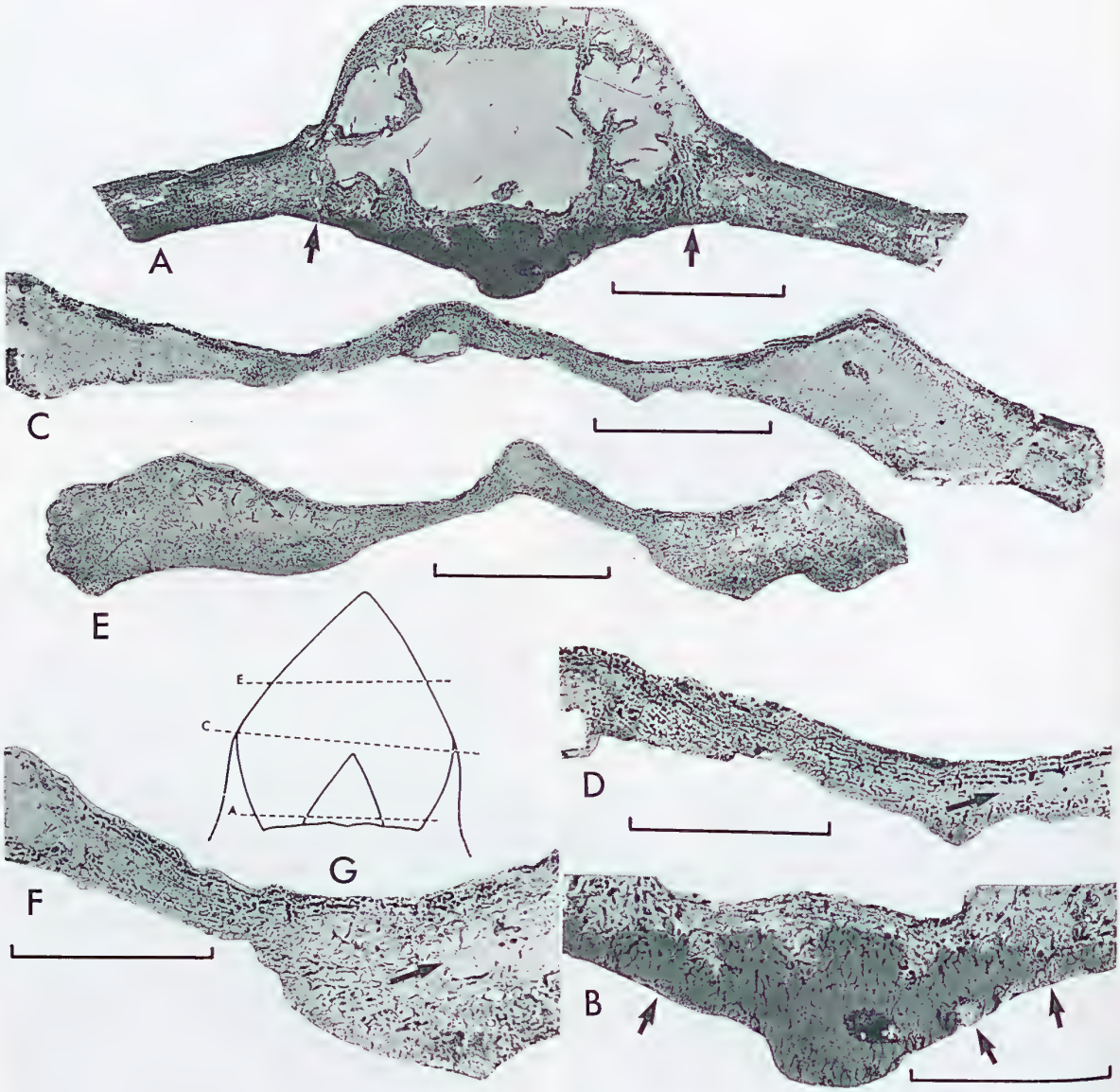

Fig. 19. (A, C, E, scale bars = 10 mm; B, D, F, scale bars = 5 mm). **A–F:** Cross sections of a palate, CPC25739, at positions shown in G. A, shows a section through the high, lightly ossified parasphenoid (boundaries marked by arrows), and the dark hard compact dentine of the posterior median callosity. C and E show the thin central part of the palate produced by extensive resorption on the buccal surface. Compression of such specimens would produce cracking along the junction between the medial thin region and the lateral thick regions, thus simulating a long narrow parasphenoid (e.g. in *Uranolophus* Denison, 1968). The large medial space in C is the result of loss during preparation of the section. B, D and F show enlargements of parts of A, C and E. B shows detail of the median callosity. (Note especially the disruption of the bone lamellae by the dentine, and the superficial dentine layer that has overgrown the callosity at the points marked by arrows.) F and D show the new continuous bone layers on the dorsal surface, the disrupted resorbed layers on the ventral surface, and the large open vascular spaces in the thicker lateral parts of the pterygoids (arrowed).

1983). However, Miles (1977) and Campbell & Barwick (1983) acknowledged that large teeth (cusps and tusks) have a rudimentary radial arrangement on both the palate and prearticulars, and that in *H. gogoensis* they interlock around the lateral margins. Further, Campbell & Barwick (1983) suggested that *Holodipterus* showed the short-headed titurating mode of feeding, and approached the gross morphology of a primitive tooth-plated genus. They suggested that it had developed this simulated tooth plate from the denticle-shedding form. A similarity with the tooth plates of *Fleurantia* was noted, a point that should be reconsidered in the light of the information on histology presented here.

Fleurantia has a subradial array of teeth disposed similarly to those of tooth-plated genera, though they are generally smaller. On the other hand, the genus has a very thin, arched palate that is covered with small denticles as far back as the posterior end of the tooth array. Denticles occur between the tooth rows. Teeth at the proximal ends of the rows have been shed and, within the spaces thus created, many new denticles have grown. This was particularly well described by Graham-Smith & Westoll (1937: 249–252). As a result of this process, the radial tooth array moved anterolaterally on the pterygoid and was replaced on the lingual side by shedding denticles. This is quite comparable to the situation in *Holodipterus*.

Fig. 20. Bright field micrograph of a region of older worn dentine at the lingual surface of the tooth base, in which translucent compact hard dentine has completely joined onto the bone. This contrasts with the region at the opposite margin, the labial side (Fig. 11A).

Though not explicitly stated by any author, the reasons for considering *Fleurantia* to be a member of the non-tooth-plated group are: the small size of the teeth; the tooth shedding so that a 'plate' in the sense of a *Dipterus* plate was not developed; the long-snouted form of the skull with the large lateral embayments suggesting relationship to *Griphognathus* and *Soederberghia;* the thin ptergyoidal bone that suggests a light bite unlike that of the usual tooth-plated types; and the ability of typical denticulated types such as *Griphognathus* to produce enamel-covered, tooth-like structures in a marginal row, though not in any predetermined radial pattern. Considerations such as these seem to have led Miles (1977: 299) to conclude that "the rows of teeth on the palate in *Fleurantia* and *Holodipterus* have a functionally determined orientation, and they tell us nothing about the phyletic relations of these forms". Such a conclusion, of course, does not mean that he considered these genera to be tooth-plated, but rather that within the non-tooth-plated group their relationships could not be determined on the basis of tooth patterns.

An alternative approach would be to consider the presence of radiate tooth rows in *Holodipterus* to be indicative of a relationship with primitive tooth-plated genera such as *Speonesydrion,* a genus that was described subsequent to Miles's account. Primitive pterygoidal tooth plates met in the midline, forming a continuous dentine sheet that covered the anterior end of the parasphenoid as well as the pterygoids, and added to their lateral margins by the incorporation of small irregular denticles. Primitive prearticular tooth plates had large callosities on the heel and denticles in the lingual furrow. *Holodipterus* dentition shares some of these characteristics, and those that it lacks could be derived by a number of changes, some relatively minor, but others requiring qualitative innovation. These include the production of mechanisms for: growth of more regular marginal denticles; resorption of old teeth from the palate and prearticulars, and replacement with shedding denticles; deposition of the superficial dentine layer that engulfed denticles and tooth bases; growth of palatal callosities; and systematic reduction of palatal thickness.

One way of examining these possibilities is to analyse the histology of the dental tissues and the morphology of the structures related to food reduction. This is done in the following section.

Relationships of *Holodipterus*

The gross structure of the whole dental apparatus, the morphogenetic sequence involved in its

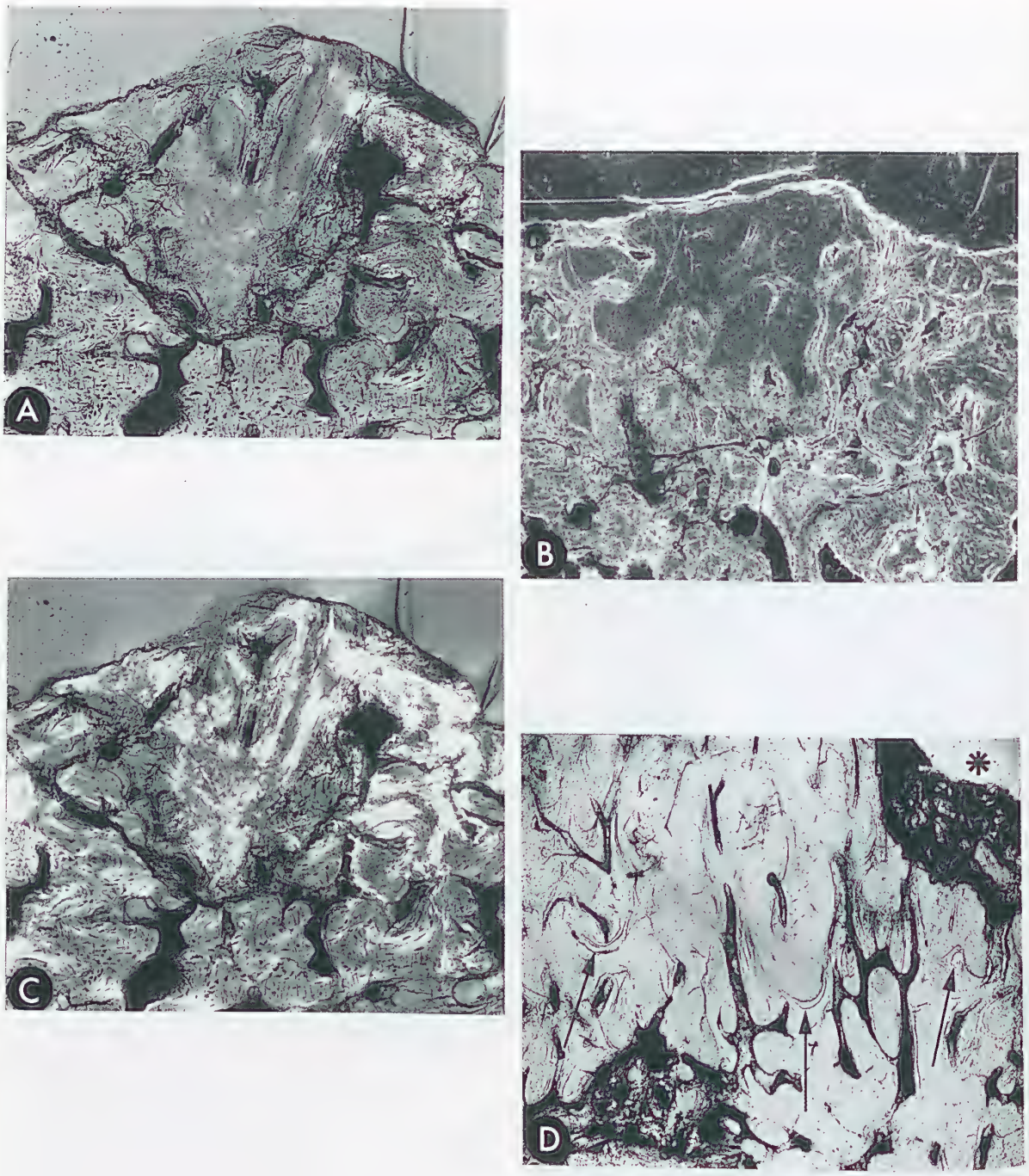

Fig. 21. A–C: (x 70) Vertical section through one of the paramedial callosities with a worn smooth surface and no covering denticles. The dentine of the callosity is translucent in ordinary light (A), and exhibits coarse, woven birefringent bands in polarized light (C). B shows a similar section through part of the callosity taken in phase contrast which emphasises the translucency of the hard compact dentine. **D:** (x 35) A region of the callosity in which pulp canals run vertically through the central part from larger spaces within the bone. In several zones (arrows) there are growth lines conforming with the shape of the forming surface. The surface of the callosity to the right shows evidence of a resorptive phase prior to growth of superficial dentine onto this surface (asterisk). CPC 25739

formation, and the histology of some of the tissues, are all unique. In the absence of any modern form to use as model, or even any post-Devonian form that could be used to provide a perspective on the evolution of this dental type, we are restricted to an analysis of characters held in common by *Holodipterus* and more primitive dipnoans in attempting to propose relationships of the genus. It is necessary to compare *Holodipterus* with both dental-plated genera and denticulated genera as the two major types. Within dental-plated genera we have discussed the existence of two types – those with dentine plates and those with tooth plates (Smith & Campbell, 1987). In the following section we discuss whether the dentition of *Holodipterus* should be considered to be a distinct type, or a modification of one of the previously defined types.

Unique features of dentition of *Holodipterus*.

SUPERFICIAL DENTINE LAYER. The extensive superficial dentine layer is not comparable with the thin layer of dentine on the palatal surface of *Dipnorhynchus* (or presumably *Speonesydrion* which is poorly known in this respect) either in its histology or its development. That is: it has a simple structure with few tubules; was formed as an infill between denticles; grew over the surface of partly resorbed older dentine as well as bone; and was itself subject to episodic resorption.

REMODELLING MODE. The episodic remodelling involved all dental tissues – the superficial dentine layer, denticles, callosities and teeth – essentially every structure situated within an advancing resorption 'front'. This distinctive remodelling was accomplished by a specific sequence of events – first the growth of a thin layer of new trabecular bone immediately behind the resorption edge, the development of denticles within this bone, the growth of superficial dentine, and finally the replacement of the superficial layer by pleromic ingrowth.

POSITION OF NEW BONE ON DENTINE. The growth of new bone and associated denticles is remarkable because it formed, in part, over the partially resorbed

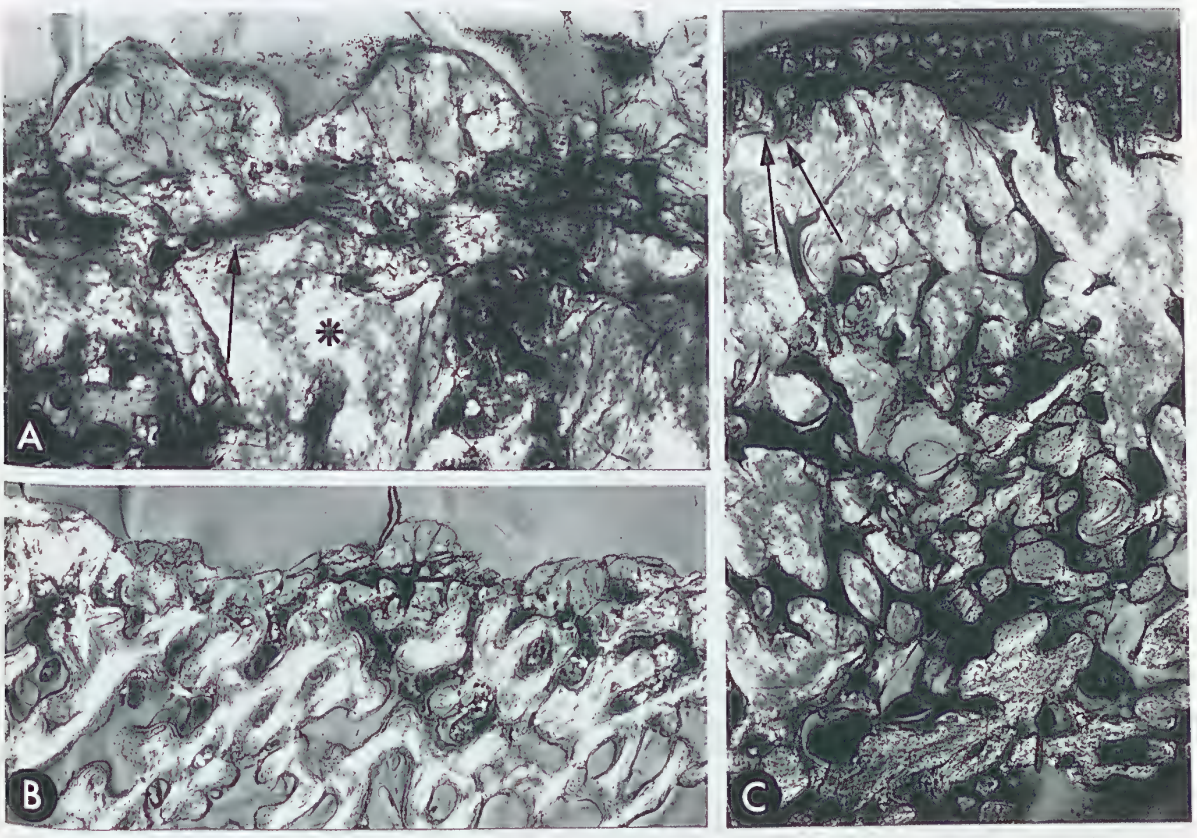

Fig. 22. **A:** (x 85) Two newly formed denticles on top of a resorption surface (arrow) formed on the compact hard dentine (asterisk). **B:** (x 35) A layer of denticles forming a thin covering to the trabecular bone, shown in partially cross polarised light. **C:** (x 40) (Field from the right of Fig. 21D.) A layer of the poorly mineralized superficial dentine overlying a resorption surface (double arrow) of hard compact dentine. The latter tissue has distinctive birefringence in cross-polarized light. CPC 25739

hypermineralised dentine that makes up the callosities.

MARGINAL DENTICLES. The development on the vertical lateral faces of the pterygoids and the prearticulars of large denticles that became overgrown and incorporated in the new bone, only to become resorbed during subsequent remodelling, is apparently unique. These accessory denticles provided an initial holding surface against which the most lateral teeth in the opposite jaw could be opposed during the subsequent growth phase. *Speonesydrion* had denticles at the margins of the prearticulars, and *Dipnorhynchus* had denticles around its pterygoids, but none of these denticles were submerged by bone during lateral growth. In *Speonesydrion* some of them came into contact with the tissues of the opposing plate, but in *Dipnorhynchus* none of them did. For present purposes it is sufficient to note that they may be regarded as only superficially similar to the lateral denticles of *Holodipterus*. Alternatively they may be regarded as primitive features that do not indicate a close relationship between the genera that carry them.

MODE OF TOOTH ADDITION. The teeth were added in sites adjacent to the short tooth rows along the lateral margins of the pterygoids and the prearticulars in alternate phases. Moreover, teeth were not added at the ends of all rows at each growth phase. Smaller teeth were added more frequently to successively more posterior rows. These features are unknown in any other dipnoan, but because uncrushed complete heads are very rare, it is impossible to say that they do not occur. However, it is possible to conclude from

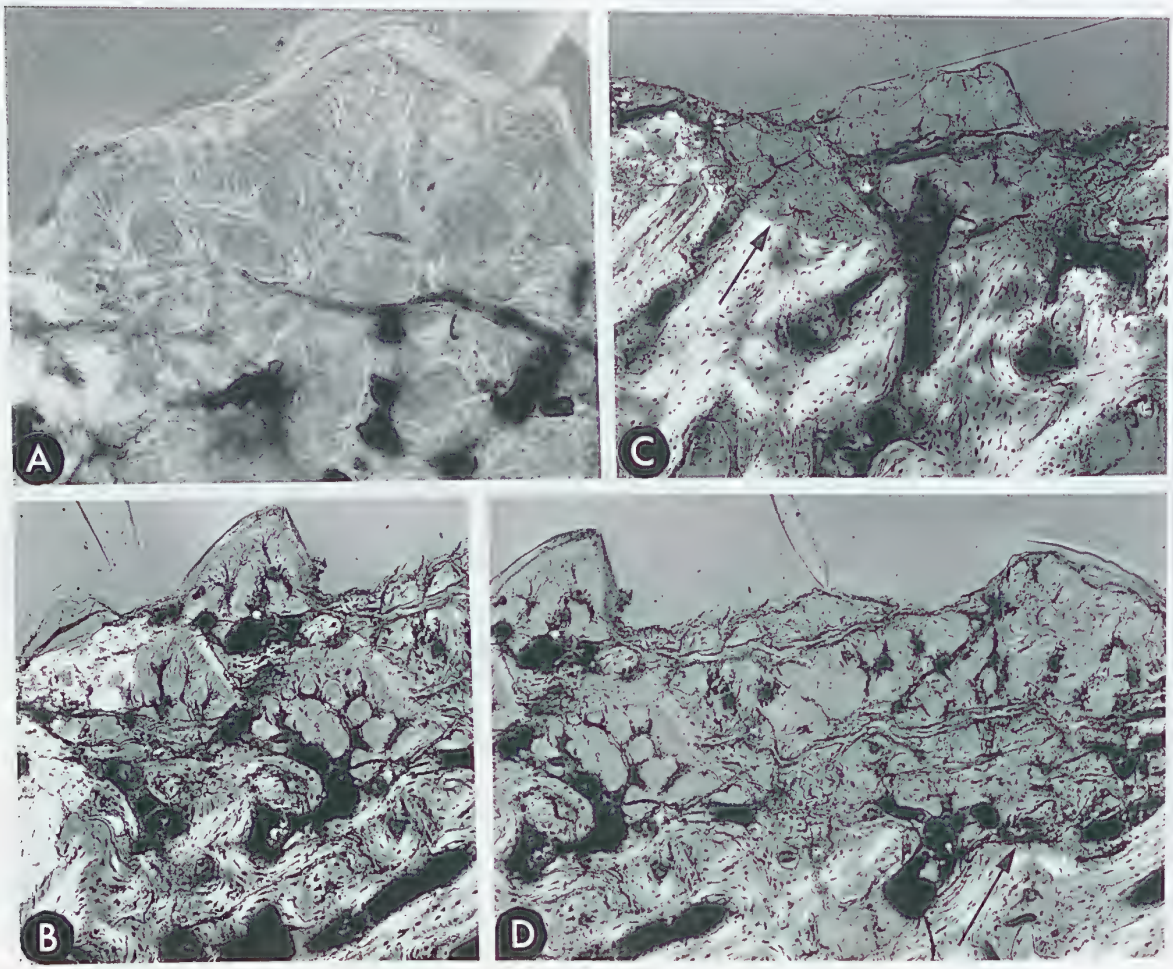

Fig. 23. **A:** (x 220) A superficial denticle, with a simple structure of many small pulp canals with arborescent terminal branches, beneath an enamel layer. **B–D:** (x 85) Section through the layer of superficial denticles with denticles superimposed, and all growing from a resorptive surface of the bone (arrows), most clearly seen as distinct tissues by their different birefringences in cross-polarized light (C). The pulp canals of the denticles are seen to be continuous with the medullary spaces of the bone. CPC 25739

the mode of growth of isolated tooth plates in such genera as *Sagenodus, Ctenodus* and *Gnathorhiza,* that they increased laterally in the same manner as the plates in *Neoceratodus,* and that this mode was not similar to that of *Holodipterus. Dipterus* and *Speonesydrion* are ambiguous in this respect. The only possible way to show a similarity to these genera would be via the discovery of some individuals with teeth overhanging the margins and others with bone extending well beyond the most lateral teeth, but bearing denticles along the lateral surfaces. So far as we are aware such specimens have not been observed. As we have shown elsewhere (Smith & Campbell, 1987), chirodipterids did not add true teeth, and so they provide no comparison. We conclude that among all the dipnoan genera known at present, *Holodipterus* is unique in this respect.

Features of *Holodipterus* dentition shared with tooth-plated genera. PRESENCE OF TRUE TEETH. *Holodipterus* has enamel-covered teeth that were added at the labial plate margins. In form and position these teeth are entirely comparable with those of normal tooth-plated genera such as *Speonesydrion, Dipterus* and *Ctenodus,* though in histological detail they show distinctive features.

Using the analogy of tooth plate growth in extant genera, Reif (1982) concluded that each tooth was formed in a dental lamina and that each tooth ridge is homologous with a tooth family in other vertebrates. The concept has been amplified in a study of the larval teeth of *Protopterus aethiopicus* (Smith, 1985). According to this model, new teeth are added to each family at the labial end. Although she did not use the tooth family concept in this sense, Kemp's work (1977) on larval *Neoceratodus* shows that the same mechanisms of plate growth are used by that genus. The presence of true teeth in *Holodipterus* could be used to imply the presence of a dental lamina. This could then be considered to be an argument in favour of relating *Holodipterus* to tooth-plated genera. For example, *Holodipterus* and *Speonesydrion* could be regarded as sharing the character of true teeth added in a regular pattern at the labial margin (see below for further discussion).

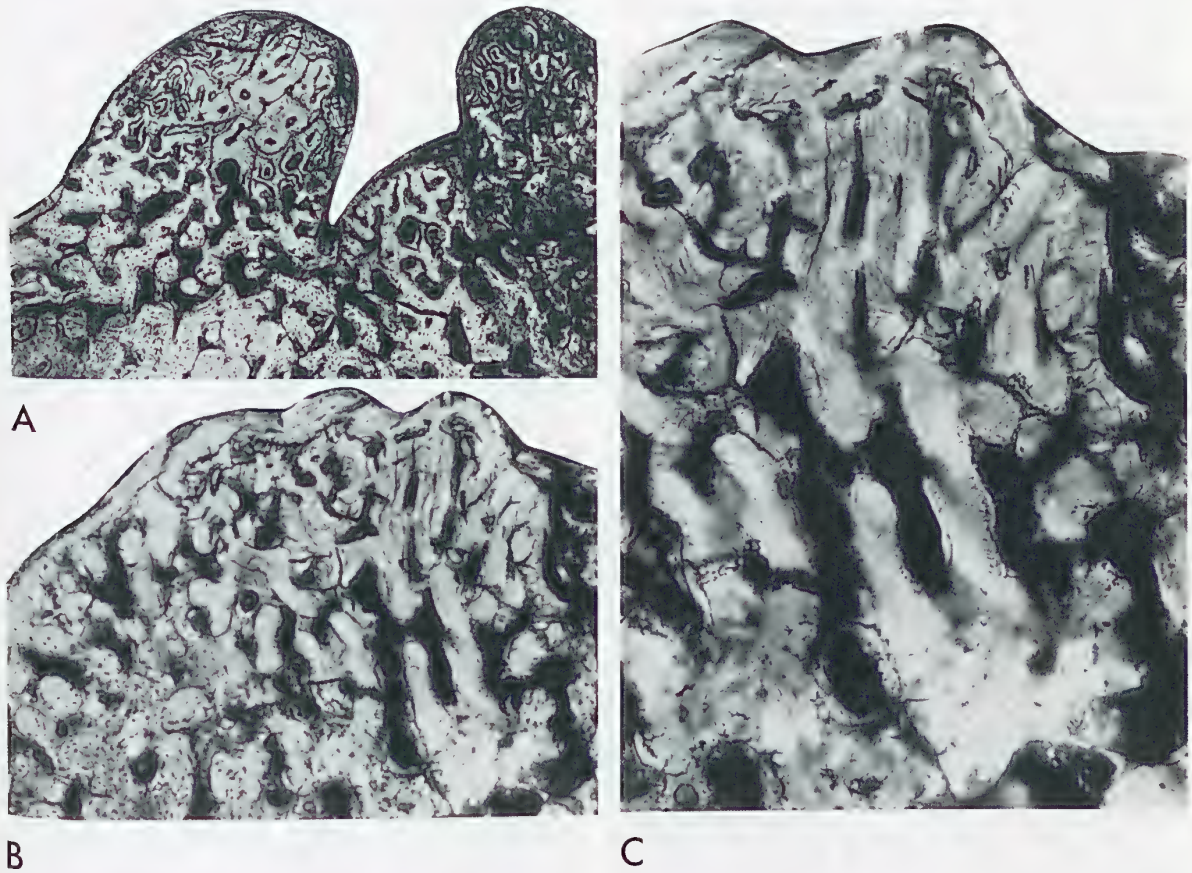

Fig. 24. **A:** (x 35) Two of the larger marginal denticles overlapping the base of a third showing a relatively compact structure to the dentine and a thin enamel layer (dorsal direction to left). **B** (x 85), **C** (x 160): one of this type of denticle to show the forming trabecular dentine at the base and poorly differentiated regions of circumpulpal dentine. CPC 25739

The force of the argument lies in the sharp distinction it makes between 'tooth' structures formed in dental laminae at predetermined positions, and 'tooth-like' structures formed superficially in any possible position without restriction to tooth primordial tissue as in a dental lamina. It would be necessary to assume that such dental laminae arose only once in the Dipnoi, and that genera with true teeth form a monophyletic group. It should also be noted that some forms with dental plates do not have true teeth, for example *Chirodipterus* (Smith & Campbell, 1987).

HYPERMINERALISED DENTINE OF TEETH AND CALLOSITIES. The teeth and callosities of *Holodipterus* are formed of translucent, compact, hard dentine that shows the cross-hatched structure under crossed polars, and the pattern of crystal-fibre-bundles in S.E.M., typical of petrodentine. However, it shows some differences from typical petrodentine, particularly in its mode of growth. The petrodentine of extant dipnoans has a characteristic structure in the region where it is formed along the edge of the pulp cavity, and this is not the structure observed in *Holodipterus*. In addition, in extant forms the regions of petrodentine between the pulp canals are not separated by homogeneous tissue that increases in thickness towards the pulp cavity, which is the arrangement in *Holodipterus*. The interpretation of the growth and significance of this tissue is problematical.

As we have concluded in the section on histology, the hypermineralised dentine in the teeth of *Holodipterus* is similar to petrodentine but not identical to it. Insofar as true petrodentine has been found only in dipnoans with dental plates, the above evidence may be used to support the view that *Holodipterus* is related to that group. If so, the different compact hard dentine, and the presence of the distinctive homogeneous tissue found in interstitial positions, suggest that it is not a normal member of the group. If, however, *Holodipterus* is related to *Speonesydrion* because they both are regarded as having true teeth, these histological differences can be explained as the result of independent development.

CALLOSITIES ON PREARTICULARS. The heel of the prearticular produced a prominent callosity very similar in appearance to that of *Speonesydrion* and *Dipnorhynchus*. In these latter genera the callosities are not well understood, but they must result from pleromic growth of hard tissue associated with wear of the surrounding regions. The prearticular callosity in *Holodipterus* grew in the same way as the callosities on the palate – that is, it resulted from downward and lateral growth of the hypermineralised dentine from a residual body of that tissue that had been considerably altered by resorption during successive phases of development. This is different from the mode of growth of the heel in the other two genera, in which no such surface resorption phases were involved.

We draw attention to the fact that in none of these genera do the heels of the prearticulars come into contact with the pterygoid plates; a large gap remains even at full occlusion. Such a relationship provides space to crush larger items of food prior to moving them towards the labial plate margins for further reduction. It would not be surprising if large callosities developed independently in several groups to serve this function.

RETAINED DENTICLES OVERLYING CALLOSITIES. Denticles that are normally shed are sometimes incorporated into the retained dentine forming the callosities in *Holodipterus*. In *Speonesydrion*, denticles are incorporated at the advancing dentine margins as a normal means of tooth-plate growth; and in *Uronemus*, a genus bearing modified dental plates, the developing elongate tooth ridges occasionally trap one or more of the shedding denticles so that they are incorporated into the retained ridge. It may be thought that the involvement of such denticles in permanent dentine formation provides grounds for relating these genera. However, once again the processes involved were quite different. In *Uronemus* the dental epithelium advanced over some adjacent denticles before they could be shed, which was their normal fate before an advancing depositional front. Their entrapment was abnormal and the ridge would have developed even if entrapment had not occurred. In *Holodipterus* the denticles were covered with superficial dentine, then subsequently they became involved with pleromic growth and were not resorbed. Only then did they contribute to the growth of the callosities which would not have been initiated, and could not have expanded, without their contribution.

Features of *Holodipterus* dentition shared with denticulate genera. SHEDDING DENTICLES. *Holodipterus* has shedding denticles of the *Uranolophus* and *Griphognathus* type on the pterygoids and prearticulars. We need to make a clear distinction between the denticles of the type found in the lingual furrow of *Speonesydrion* and those of the above genera. As has been well shown by Smith (1977), the denticles of *Griphognathus* were shed and regrown at irregular intervals on an irregular pattern during the life of an animal. If they were incorporated into the marginal ridges they were subsequently lost when these tissues were resorbed during remodelling. The denticles of *Speonesydrion* were not lost in this manner, but continued to grow until they were incorporated into the advancing dentine front that formed a tooth plate. The same is true of the denticles in the lingual furrow and on the posterior part of the pterygoids and the parasphenoid of *Dipnorhynchus*. The denticles of *Holodipterus* are simple, like those of *Griphognathus*, and most of them were shed, although during certain phases of growth those that had not been shed were overgrown by bone, simple

dentine, or more denticles, and thus were temporarily retained on the dental surface until the next phase of resorption took place. The exceptions to this are the callosities on the palate and the prearticulars, but these do not form parts of tooth plates.

As indicated above, at least one tooth-plated genus, *Uronemus,* has on the pterygoids denticles that were shed, although they have a more complex histology than those of *Griphognathus.* Further, many other groups of gnathostome fishes have denticles that are shed. The argument is regularly advanced that such a condition is primitive (Nelson, 1969) and therefore is not of significance in determining relationship. This is a superficial judgement. In the first place, *Uronemus* is an advanced genus in which the tooth plates have retreated to a lateral position, exposing the surface of the pterygoids in the buccal cavity. Much of this surface was then adapted for the appropriate positioning of the 'tongue-pad' during buccal pump action, as an essential part of the air-breathing process. The remainder of the surface became covered with shedding denticles which functioned as an essential part of the distinctive shearing bite of the genus (Smith, Smithson & Campbell, 1987). In other words, the denticles of *Uronemus* are secondarily developed for a specific function. This conclusion does not deny the proposition that the capacity to develop such denticles is a primitive feature of the epithelium. What it asserts is that this capacity was retained but not necessarily expressed in advanced forms. It was expressed when the need arose. This points up once again the fallacy of categorising a structure as primitive or advanced without a consideration of the developmental and evolutionary processes involved in its formation. Such a fallacy results from failure to take into account the variety of morphological, histological and functional data available, while concentrating on apparent similarities of physical entities, in this case, denticles. It ignores the complexity and richness of the biological system by treating the products of such processes as though they were inorganic entities whose relationships are to be determined by the application of principles appropriate to inorganic processes. Further, it is no response to this criticism to suggest that all that is required is a refinement of the character analysed – that is, denticles with a certain disposition on the pterygoids rather than denticles in general. In the first place one has to perform a preliminary developmental, functional and stratigraphic analysis to appreciate that a feature is significant. In the second place it could always be claimed that the denticles indicated that the organism was primitive in this respect, unless it was appreciated that the main issue is the capacity of the epithelium to produce denticles at points of functional necessity, and not the presence of the denticles themselves. The issues of the argument are the identification of the character to be analysed, the relation of that character to surrounding observed and inferred soft tissues, and the history of the character through geological time. None of these issues are even approached by a method that excludes a thorough biological analysis prior to an attempt to infer taxonomic significance.

Remodelling of Marginal Structures. A feature of the marginal structures of *Uranolophus* and *Griphognathus* is the extent to which they are resorbed and remodelled during growth. Juveniles of *G. whitei* have a number of short, anteriorly directed ridges on the anterior part of the palate (Campbell & Barwick, 1983: figs 16–17) but these were subsequently lost and replaced by a variety of temporary ridges and tuberosities. The marginal ridges, which occur on both the pterygoids and the prearticulars, are very varied in form, and do not produce a regular persistent pattern. *Uranolophus* has more or less continuous marginal ridges on the pterygoids and prearticulars, and these were apparently totally resorbed and regrown at certain stages of development (Denison, 1974). In both these genera, this marginal remodelling permitted the lateral expansion of the denticulated surfaces of both pterygoids and prearticulars. This is also a feature of *Holodipterus.*

Presence of Basihyal/basibranchial Dental Plates. *Holodipterus gogoensis* probably had basihyal/basibranchial dental plates. Though dental plates are rarely preserved, this should not be taken as evidence that they are not always present. Specimens of the species are not common, and they are almost always disarticulated. The dental plates would have fallen free and, even if found, would not be recognised as belonging to the species. In addition, the palates themselves show evidence of the presence of dental plates on the basihyal/basibranchial system because the posterior medial palatal callosities are usually worn smooth and some show a polish.

A most important feature in this regard is the disposition of the tooth rows in the mandible. Devonian genera of the dental-plated type *(Dipterus, Chirodipterus, Scaumenacia, Speonesydrion)* have the lingual tooth rows on the prearticulars well medial of the limits of the posterior ends of the dentary. The lingual space is obviously limited. However, *Holodipterus gogoensis* has the lingual rows on the mandible aligned with the ends of the dentary, thus leaving a large lingual space. This is similar to the arrangement in *Griphognathus whitei* in which the marginal ridges of the prearticulars and the ends of the dentary are confluent. The lingual space was occupied by the basihyal/basibranchial system. Thus the pattern in *H. gogoensis* is consistent with, though it does not prove, the presence of such a system.

Taken together, the presence of isolated pieces of denticulate tooth plate, the median callosities that sometimes have a polished surface, and the disposition of the tooth rows, strongly suggest the presence of a basihyal/basibranchial system such as is

found in the typical denticulate genus *Griphognathus*.

MEDIAN CALLOSITIES. Many denticulated species do not have median callosities, but they are known on one specimen of *Uranolophus wyomingensis* where they presumably served the same function as in *Holodipterus*. Callosities in denticulate species result from the pleromic growth of dentine and the failure to resorb tissue that is normally shed. It is worth noting that some of the palatal tusks of *Griphognathus whitei*, though not situated medially (see Campbell & Barwick, 1986: fig. 4B) are formed by precisely the same process. They are not present in some specimens of that species because resorption has completely removed them.

PALATAL SHAPE. A feature of the dentition of members of the denticulated lineage is the high arch of the palate and the extension of the denticulation over the whole surface of the pterygoids and the anterior part of the parasphenoid. This is known in *Uranolophus, Griphognathus, Soederberghia, Jarvikia* and *Conchopoma*. Such a distribution is related to the presence and position of the basihyal/basibranchial tooth plates. *Holodipterus gogoensis* is a normal member of the lineage in this respect; *Fleurantia*, usually put with this group, may be an exception, and further work on the genus is necessary.

CHARACTERISTIC CHEEK POUCH. The extant genera *Protopterus, Lepidosiren* and *Neoceratodus*, all of which have tooth plates, break down their food in a distinctive way. After sucking a piece of food into the mouth, it is pushed out again in short movements by the action of the tongue-pad. After each forward projection the food is bitten by the anteriorly placed tooth plates. The partly pulverised food is held together by a mass of stringy mucous. After complete expulsion, the food and mucous are sucked back into the mouth. The process is repeated several times.

This mechanism could be effective only if a tongue-pad (or perhaps a modified part of the basihyal apparatus) was placed far enough forwards to eject the food, and the tooth plates were able to bite it as it was ejected. It is unlikely that such denticulated genera as *Griphognathus* had a tongue pad that could perform such a function because the basihyal/basibranchial apparatus itself would preclude such an arrangement, and they certainly had no anteriorly placed dental plates. Presumably they had adopted some alternative means of recycling food through the buccal cavity or they ate food that did not require chewing. The presence of the basihyal/basibranchial dental plates suggests that the latter proposal is not correct. In addition to this, the dentition of such forms consisted of lateral marginal ridges and denticles of various kinds indicating that food would have been passed laterally rather than forwards. This is consistent with the view of Campbell & Barwick (1983) that genera such as *Griphognathus* and *Soederberghia* had large muscular cheek pouches into which the food was passed. The cheeks of contemporaneous tooth-plated genera such as *Dipterus* and *Chirodipterus* were covered with dermal bones that left no space for such pouches.

Although the roofing and cheek bones of *Holodipterus* are poorly known, one specimen in the British Museum (Natural History), P524568, is sufficiently well preserved to show the characteristic profile of the cheek bones (Fig. 8). This is of the *Griphognathus* type rather than the *Dipterus* type, and is therefore consistent with the interpretation of *Holodipterus* as a genus without an anteriorly placed tongue-pad, and with a feeding mechanism typical of the denticulated lineage.

CONCLUSIONS

Many of the aspects of the dental tissues of *Holodipterus gogoensis*, and the processes that produced them, are unlike those of any other dipnoan that has been studied in detail. The most unusual features are the superficial layer of simple dentine, the resorption of all types of dental tissues including those forming the teeth, the growth of new bone and dentine over the remaining unresorbed hypermineralised dentine forming the callosities, the mode of pleromic infill of the superficial layer, the pleromic mode of growth of the callosities, the cyclical addition of teeth in a distinctive sequence, and the structure of the dentine forming the main mass of the teeth. Differences between specimens are considerable, and result, at least in part, from the death of individuals at different stages of the resorption/remodelling cycle. Comparative work on species of this genus obviously has to be based on a growth sequence.

We have attempted to examine the features of the dentition that would allow us to relate *Holodipterus* to tooth-plated genera such as *Speonesydrion* and *Dipterus*, or to denticulate genera such as *Uranolophus* and *Griphognathus*. The outcome of the discussion has not proved conclusive. On the one hand the presence of the marginal denticles, and radiate rows of true teeth composed of a hypermineralised tissue with some of the properties of petrodentine, may be taken to weigh heavily in favour of the former relationship. On the other hand, this proposal is weakened by: the failure to develop true tooth plates because all teeth, except those near the margin, are removed by resorption of their bases; the lightly ossified palate that is repeatedly thinned by resorption of its buccal surface; the distinctive hypermineralised dentine; the smooth lamellate dentine trabeculae in the teeth; and similarities with the tooth pattern of the denticulate genus *Fleurantia*. The suggestion that *Holodipterus* is more allied to the denticulate genera is supported by evidence of the presence of a basihyal/basibranchial dental system, the cheek structure that goes with such a system, the type and distribution of the denticles, the repeated

remodelling of the buccal tissues including the bony surface of the palate, and the fact that *Fleurantia* resorbs its teeth and replaces them with denticles.

The conclusion reached depends on one's philosophy of establishing relationships. M.M.S. accepts that the presence of true teeth implies the development of dental laminae, a primitive character linking all those dipnoans 'with teeth' and not likely to have been lost and secondarily acquired in some dipnoans (for further discussion see Smith, 1987). Hence, a relationship with primitive tooth-plated forms such as *Speonesydrion* is indicated. The many distinctive features of the dentition of *Holodipterus* imply that it evolved divergently from the more advanced Devonian tooth-plated genera such as *Dipterus* and *Scaumenacia*. K.S.W.C. prefers the view that the feeding system should be treated as a functional developmental entity, and considers that relationships with the denticulated genera are indicated; teeth would have evolved more than once in the Dipnoi. It is obvious that the structure of *Fleurantia*, a generally acknowledged member of the denticulate group, is important for the above argument, and work on the precise details of its dental development and histology is now required. In addition, other characters of the two genera, particularly the basihyal/basibranchial systems, need further study.

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References

Bassett, C.A.L., 1971. Biophysical principles affecting bone structure. **In** "The Biochemistry and Physiology of Bone". (G.H. Borm ed.) Vol. 3: 1–76. Academic Press, London.

Baume, L.J., 1980. The biology of pulp and dentine. A historic, terminologic, taxonomic, histologic, biochemical and clinical survey. Monographs in Oral Science, 8. S. Karger, Basel.

Campbell, K.S.W. & R.E. Barwick, 1983. Early evolution of dipnoan dentitions and a new genus *Speonesydrion*. Memoirs of the Association of Australasian Palaeontologists 1: 17–49.

_____ 1987. Paleozoic lungfishes – a review. Journal of Morphology Supplement 1: 93–131.

Denison, R.H., 1974. The structure and evolution of teeth in lungfishes. Fieldiana: Geology 33: 31–58.

Graham-Smith, W. & T.S. Westoll, 1937. On a new long-headed dipnoan fish from the Upper Devonian of Scaumenac Bay, P.Q., Canada. Transactions of the Royal Society of Edinburgh 59: 241–256.

Kemp, A., 1977. The pattern of tooth plate formation in the Australian lungfish, *Neoceratodus forsteri* Krefft. Zoological Journal of the Linnean Society of London 60: 223–258.

Miles, R.S., 1977. Dipnoan (lungfish) skulls and the relationships of the group: a study based on new species from the Devonian of Australia. Zoological Journal of the Linnean Society of London 61: 1–328.

Nelson, G., 1969. Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. Bulletin of the American Museum of Natural History 141: 475–552.

Reif, W.E., 1982. Evolution of dermal skeleton and dentition in vertebrates: the odontode regulation theory. Evolutionary Biology 15: 287–368.

Smith, M.M., 1977. The microstructure of the dentition and dermal ornament of three dipnoans from the Devonian of Western Australia: a contribution towards dipnoan interrelations, and morphogenesis, growth and adaptation of the skeletal tissues. Philosophical Transactions of the Royal Society of London (B) 281: 29–72.

_____ 1979. Structure and histogenesis of tooth plates in *Sagenodus inaequalis* Owen considered in relation to the phylogeny of post-Devonian dipnoans. Proceedings of the Royal Society of London (B) 204: 15–39.

_____ 1984. Petrodentine in extant and fossil dipnoan dentitions: microstructure, histogenesis and growth. Proceedings of the Linnean Society of New South Wales 107: 367–407.

_____ 1985. The pattern of histogenesis and growth of tooth plates in larval stages of extant lungfish. Journal of Anatomy 140: 627–643.

_____ 1987. The dentition of Palaeozoic lungfish, implications for the phylogeny of dipnoans. VIIth International Symposium Dental Morphology, Paris (in press).

Smith, M.M. & K.S.W. Campbell, 1987. Comparative morphology, histology and growth of the dental plates of the Devonian dipnoan *Chirodipterus*. Philosophical Transactions of the Royal Society of London (B) (in press).

Smith, M.M., T.R. Smithson & K.S.W. Campbell, 1987. The relationships of *Uronemus* – a Carboniferous dipnoan with highly modified tooth plates. Philosophical Transactions of the Royal Society of London (B) (in press).

APPENDIX

Dentine terminology is still in a state of flux, despite several recent attempts to clarify some specific points (Smith, 1979, 1984, 1985). To some extent the variety of terms reflects the diversity of dental tissues found, in particular, in the dentitions of Palaeozoic lungfish. The tissues of *Holodipterus* show specific features for which it is necessary to give our definitions in this paper. Reference should also be made to the three articles listed above. Note that we use the terms 'primary', 'secondary' and 'tertiary' to refer to the sequence in which the various types of dentine are formed during the growth of a tooth. The terms pallial, interstitial, circumpulpal and intrapulpal are topogenic terms (Baume, 1980: 49) indicating the site of initial formation.

Microstructure

Pallial dentine. Lightly mineralised primary dentine (i.e. the first-formed dentine in a tooth) with randomly oriented small crystals and containing the distal ends of the dentine tubules extending from the underlying more complex dentine; forms a thin layer immediately beneath the enamel cover of a tooth or a denticle; deposited from undifferentiated odontoblasts in the primary pulp cavity (derived from the mesenchymal dental papilla of the tooth germ).

Interstitial dentine. Secondary dentine occupying the space in the core of a tooth with a divided pulp cavity or a callosity between the deposits of circumpulpal dentine; sometimes continuous with the pallial dentine; usually without dentine tubules; variable levels of mineralization; may be formed from either mesenchymal cells or differentiated odontoblasts in the pulp cavity. Equivalent to the initial dentine trabeculae of intrapulpal dentine, later invested with circumpulpal dentine (denteones).

Petrodentine. A special type of intrapulpal dentine between pallial and circumpulpal dentine; hypermineralised relative to any other dentine or bone; hard and translucent; formed of crystal-fibre-bundles consisting of parallel, large hydroxyapatite crystallites; diameter and arrangement of the crystal-fibre-bundles varies amongst the genera; in extant genera arranged so that adjacent bundles (domains of crystals) alternate through 90° to each other; dentine tubules scarce, restricted to the borders with the circumpulpal dentine; formed from a special cell population (petroblasts), initially from the dental papilla, subsequently from those in the pulp cavity at the base of a tooth.

Circumpulpal dentine. Tertiary dentine with normal levels of mineralisation, composed of small crystals; traversed by numerous branching tubules; arranged as sequential layers concentric with the pulp canals in teeth where the pulp cavity is divided by infilling with dentine, or in the dentine of callosities around the vascular canals; formed from odontoblasts within the pulp canals.

Superficial dentine. Formed as a layer beneath the epithelium without division into odontodes (units of dentine, see Smith, 1979); lightly mineralised dentine with randomly oriented small crystals; traversed by short irregular pulp spaces from which extend numerous dentine tubules; pulp spaces connect directly with the medullary spaces in the underlying bone; found in sheets filling in the space between denticles on the palate and prearticulars in *Holodipterus;* similar in structure to the pallial dentine of the associated denticles.

Pleromic dentine. Dentine filling an existing medullary space in bone (or other dentine) or a space produced by resorption; always invasive in form; commonly with numerous dentine tubules restricted in their extent; frequently translucent and may be composed of crystal-fibre-bundles; typically formed as poculae (small pockets of dentine, see Smith, 1977: fig. 14) in areas of wear stress, such as callosities, or beneath and within old dentine, and denticles on pterygoids and prearticulars.

Trabecular dentine. An arrangement of dental tissue in which struts of dentine divide a pulp cavity into many large, soft-tissue compartments which may subsequently be reduced in size by further growth of dentine by apposition onto the primary trabeculae.

Compact dentine. An arrangement of dentine types leaving proportionally very small, soft tissue spaces, as pulp canals, within a dense dentine mass (frequently called osteodentine) filling in the primary pulp cavity.

Macrostructure

Denticles. Small enamel-covered dentine eminences of various shapes formed superficially on demand at any place on the palate and lower jaw at any time, wherever prior resorption makes a space that can be occupied by mesenchyme beneath an epithelium; allows a complete denticulated cover to be maintained at all times (Reif, 1982). Alternatively, similar eminences formed at the lateral margins of the pterygoids or prearticulars on top of new bone (see Smith, 1987).

Teeth. Enamel-covered cones of specialized dentine formed in specific loci at the lateral margins of the palate and lower jaw, aligned with existing older, worn teeth and initiated at predetermined times; allows alternation of sequential teeth in opposing jaws and alternation of opposing tooth rows.

Callosities. Hypermineralized, translucent dentine forming a hard, wear-resistant region raised above the denticulated surface; promoted by growth of pleromic dentine into the subjacent tissues, presumed to grow continuously and to wear less rapidly than the adjacent dental tissues; never enamel covered.

Heel. A raised area of hypermineralized dentine at the posteromedial corner of the pre-articular 'tooth plate'; similar mode of growth to callosities on the palate.

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Australian *Renocila* Miers, 1880 (Isopoda: Cymothoidae), Crustacean Parasites of Marine Fishes

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ABSTRACT. The Australian species of the genus *Renocila* are recorded for the first time. Three species are recorded: *R. ovata* Miers, *R. alkoo* n. sp., and *R. plesiopi* n. sp. *Lironeca dubia* Nierstrasz is found to be a synonym of *Renocila ovata*. The genus *Rosca* Schiödte & Meinert is placed in synonymy with *Renocila*. A synoptic list of all Indo-Pacific species of *Renocila* is given, as well as a new generic diagnosis and a key to the Australian species.

BRUCE, N.L., 1987. Australian *Renocila* Miers, 1880 (Isopoda: Cymothoidae), crustacean parasites of marine fishes. Records of the Australian Museum 39(3): 169–182.

The genus *Renocila* was previously known from Australia by a single record of an unidentified species (Healy & Yaldwyn, 1970). The genus is apparently uncommon in Australian waters there being few specimens in museum collections, while 6 weeks of field work on the Great Barrier Reef (2–4 hours under water each day) failed to obtain any fresh material.

The genus has four species in the Caribbean (Williams & Williams, 1980), and eight species in the Indo-Pacific. Of the Indo-Pacific species two, *R. periophthalma* and *R. recta,* are based on juvenile specimens which lack the species-specific characters of the adult. The status and identity of these two species are therefore uncertain. The number of species is likely to increase, for I have seen specimens of another two *Renocila* species from Australia, but lack sufficient material to describe them, while material recorded by Richardson (1910) as *R. ovata* (USNM 40494, also USNM 231172-4) is an undescribed species. The distribution of *Renocila* around Australia and Indonesia is given in Figure 9.

A key to the Australian genera of externally attaching cymothoid isopods was given by Bruce (1987). Material and methods follow that of Bruce (1987). Abbreviations used are as follows: **AM** – Australian Museum, Sydney, NSW; **BMNH** – British Museum (Natural History), London; **GBR** – Great Barrier Reef, Queensland, Australia; **NMW** – Naturhistorisches Museum, Vienna; **Qld** – Queensland, Australia; **QM** – Queensland Museum, Brisbane, Qld; **RMNH** – Rijksmuseum van Natuurlijke Historie, Leiden; **USNM** – Smithsonian Institution, Washington, D.C.; **WA** – Western Australia; **WAM** – Western Australian Museum, Perth, WA; **ZMA** – Zoologisch Museum, University of Amsterdam.

TAXONOMY

Renocila Miers

Renocila Miers, 1880: 464.—Gerstaecker, 1882: 232; Schiödte & Meinert, 1884: 415; Stebbing, 1900: 610; Barnard, 1936: 160; Bowman & Mariscal, 1968: 100; Brusca, 1981: 146.

Rosca Schiödte & Meinert, 1881: 85.—Stebbing, 1924: 10.

Type species. *Renocila ovata* Miers, 1880, by monotypy.

Diagnosis of female. Rostrum wide, anterior part folded under and back, not triangular, not projecting between antennules. Cephalon posterior margin not trisinuate. Coxae 2 and 3 as long or longer than respective pereonite; coxae 5–7 shorter than pereonite, posteriorly acute. Posterolateral margins of pereonites 6–7 produced, not narrowed or tapered. Pleonites 1–2 ventrolateral margins not produced, posterolateral margins not acute.

Antennule subequal to or shorter in length than antenna. Mandible palp articles 1, or 1 and 2

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dilated, or wider than article 3; article 3 slender, shorter than 2. Pleopods all lamellar except endopod of pleopod 5, which has 3 weakly developed folds.

Additional characters. Body about twice as long as wide, dorsum moderately convex. Eyes posterolateral in position, less than 0.3 width of cephalon. Pereonite 2 shortest, 5 and 6 longest; pereonite 5 widest; coxae visible in dorsal view. Pleotelson always flat.

Antennule dorsoventrally compressed; antenna less robust than antennule; bases widely separate. Maxillule with 4 or 5 terminal spines. Maxilla with 2 small spines each on medial and lateral lobe respectively. Maxilliped article 3 with 3 or 5 terminal spines. Pereopods 1–4 subequal in length, 5–7 slightly longer than 1–4; pereopod 7 not manifestly longer than pereopod 6 (except in *R. ovata).* Brood pouch consisting of alternately overlapping oostegites arising from the base of pereopods 1, 2, 3, 4 and 6; posterior enclosed by laminar fold arising from posterior of sternite 7. Endopods of pleopods 3–5 with prominent proximomedial lobes. Uropod exopod longer than endopod, rami usually concealed beneath pleotelson.

Male. Smaller, narrower than female; eyes proportionally larger. Uropods conspicuous, projecting beyond pleotelson. Appendages similar to female except: antennule not as robust; mandible palp more slender, article 1 not dilated; maxilliped article 3 with larger terminal spines; pereopod dactylus nodules and basis carina not developed. Pleopod 2 with appendix masculina; folds on pleopod 5 endopod weakly developed. Penial processes present, on posterior of sternite 7.

Remarks. Characters that separate *Renocila* from related genera are: antennule longer and more robust than antenna; rostrum not projecting between antennules; pleonites 1–2 with ventrolateral margins not produced; posterolateral margins of pereonites 6–7 produced; uropods held concealed beneath pleotelson. In addition, *Renocila* are wider than most *Anilocra,* although at least two species of *Anilocra (A. amboinensis* and *A. pomacentri)* approach the shape shown by *Renocila.*

Pleopod morphology, included in the genus description, applies only to the species described here, and *Renocila threshorum* Williams & Williams (figured by Brusca, 1981). No other *Renocila* species have had their pleopods described.

The Caribbean and east Pacific *Renocila* differ in several morphological characters from the Indo-Pacific species, lacking the carinate process on the posterodistal margin of the basis of pereopods 1–3, having mandible palp articles 1–2 not expanded, mandible palp article 3 more setose, lacking any trace of pereopodal nodules (present or absent in Indo-Pacific species), and one species *(R. colini)* with the antennule shorter than the antenna.

Examination of the holotype of *Rosca limbata* Schiödte & Meinert (RMNH 6) revealed it to be an immature *Renocila* specimen. Similarly, the material recorded by Nierstrasz (1931) (ZMA uncatalogued) is also an immature *Renocila.* Only one other species has been placed in *Rosca: Rosca rogans* Stebbing, 1924, is an immature intermoult *Nerocila* (see Bruce, 1987). Trilles (1979) recorded two ovigerous females of *Rosca limbata,* but as this material was not available for study no comment can be made on their identity.

Bruce (1987) provided a key to the Australian genera of externally attaching cymothoid isopods.

Synopsis of Indo-Pacific *Renocila*

Renocila heterozota Bowman & Mariscal, 1968. Types at USNM 113431-113433, Mahé, Seychelles, on *Amphiprion akallopisos.*

Renocila indica Schiödte & Meinert, 1884. Holotype held at NMW number 5278. Indonesia, hosts unknown, additional figures provided (Fig. 1).

Renocila limbata (Schiödte & Meinert, 1881), **new combination.** This species has been little recorded (see Trilles, 1979), and the adult female has not been described. Recorded hosts: *Scorpaena picta* (by

ISOPOD	HOST		DISTRIBUTION
R. heterozota	Pomacentridae	*Amphiprion akallopisos*	Seychelles
R. indica	not known		Indonesia
R. limbata	Scorpaenidae	*Scorpaena picta**	Indonesia
		*Sebastopsis polylepis**	Indonesia
R. ovata	Pomacentridae	*Eupomacentrus fasciolatus*	Carnarvon, WA
R. periophthalma	Periophthalmidae	*Periophthalmus* sp.*	Lifu, Loyalty Islands
R. plesiopi	Plesiopidae	*Plesiops corallicola*	Swains, GBR
	Apogonidae	*Apogon* sp.	Swains, GBR
		*Apogon guttatus**	Heron Is, GBR
R. recta	not known		Indonesia
R. alkoo	not known		GBR

Table 1. Indo-Pacific *Renocila* and their associated hosts (* = unconfirmed host; GBR = Great Barrier Reef).

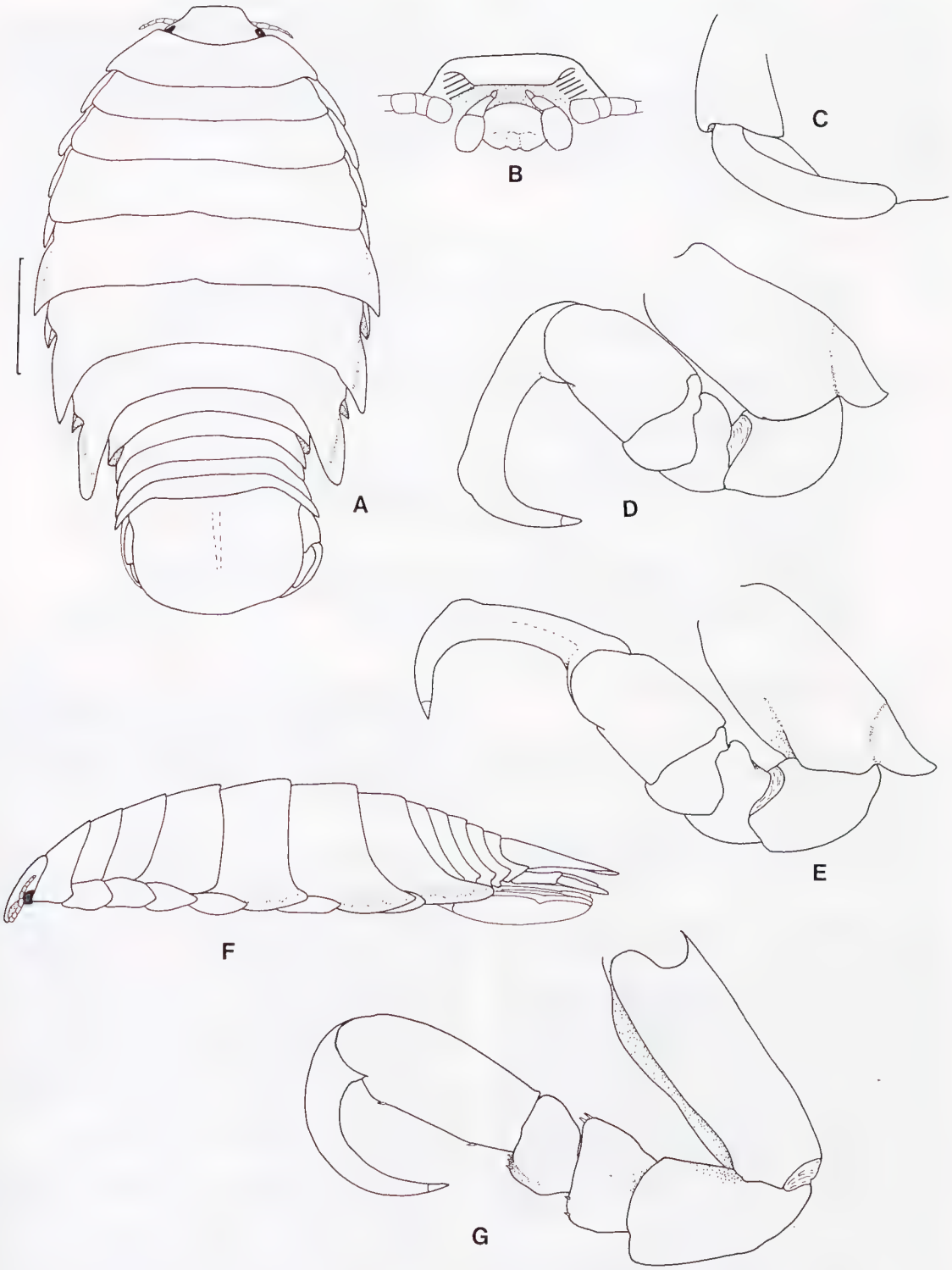

Fig 1. *Renocila indica,* holotype, NMW 5278. **A,** dorsal view; **B,** frons; **C,** right uropod, in situ; **D,** pereopod 1; **E,** pereopod 2; **F,** lateral view; **G,** pereopod 7. Scale line represents 3.0 mm.

Nierstrasz, 1931) and *Sebastopsis polylepis* (by Trilles, 1979). Localities: Sebu, Savu; Amboina; Timor; all Indonesia.

Renocila ovata. Present study.

Renocila periophthalma Stebbing, 1900. Holotype, BMNH 1906.4.19.16, Lifu, Loyalty Islands. A damaged male, with head and pereonite 1 missing; identity uncertain. Host given as *Periophthalmus* (F. Periophthalmidae – mud skippers).

Renocila plesiopi. Present study.

Renocila recta (Nierstrasz, 1915), **new combination.** Holotype RMNH 35, West Java. The species is clearly a *Renocila* (not *Anilocra),* but is an immature specimen and therefore of uncertain identity and status. Host given as *Hexanematichthyes sundiacus* (F. Ariidae).

Renocila alkoo. Present study.

Key to Australian *Renocila*

1. Pleon narrow, about 0.35 width of pereonite 5, posterolateral margins of pereonites 5–7 produced, acute; pereopods 1–2 with long smoothly curving dactylus, without nodules; pereopods 1–2 basis with posterodistal angle not produced. ..... *R. plesiopi*

—— Pleon greater than 0.5 width of pereonite 5, posterolateral margins of pereonites 5–7 not acute; pereopod 1 and 2 dactylus not as above; pereopods 1–2 basis posterodistal angle carinate, produced. 2

2. Posterolateral margins of only pereonites 6 and 7 produced, rounded; pereopods 1–2 dactylus short, abruptly recurved; pereopods 1–2 basis with posterodistal angle produced and truncate, posterior margin of ischium and merus carinate. ..... *R. alkoo*

—— Posterolateral margins of pereonites 5–7 produced, narrowly rounded; pereopods 1–2 dactylus long, abruptly recurved; pereopods 1–2 basis with posterodistal angle produced, narrowing to blunt point. ..... *R. ovata*

Renocila ovata Miers
Figs 2–4

Renocila ovata Miers, 1880: 464, pl. 25, figs 11–14.—Gerstaecker, 1882: 261; Schiödte & Meinert, 1884: 416; Nierstrasz, 1931: 126.

Livoneca dubia Nierstrasz, 1918: 116.

Livoneca dubia Nierstrasz, 1931: 138, figs 2–5, pls 10–14.

Not *Renocila ovata.*—Richardson, 1910: 22 (= undescribed species).

Material examined. LECTOTYPE, female (ovig 21.5) and PARALECTOTYPE, female (ovig 16.0), Malaysia, coll. P. Bleeker (BMNH 1880: 15).

Non-type. Female (ovig 22.5), Amboina, 1859, coll. Dr Deleschall (NMW 5276, examined by Schiödte & Meinert, 1884). Syntypes of *Livoneca dubia* Nierstrasz, 1931: female (ovig 15.0), Labuan Pandau, Lombok Reef, 27 March 1899, Siboga Expedition Stn 34 (ZMA Is. 100-602); female (ovig 10.5), Seba, Savu, 25 April 1899, Siboga Expedition Stn 58, on *Apogon* sp., coll. M. Weber (ZMA Is. 100-603). Female (ovig 10.0), Seba, Savu, 25 April 1899, on juvenile Pomacentridae sp., Siboga Expedition Stn 58, coll. M. Weber (ZMA Is. 100-604). Types of *Livoneca dubia* Nierstrasz, 1918: female (ovig 15.5), male (9.0), north coast of east Flores, 123°01.3′E, 08°09.7′S, 11 Nov 1908, coll. G.J. Van der Sande (ZMA Is. 105-055).

From Western Australia: female (ovig 21.0), Carnarvon, 24°53′S, 113°40′E, circa 1960, coll. Mr R. Walker (WAM 612-85); female (ovig 16.0), male (7.0), Point Quobba, 24°29′S 113°25′E, Oct 1959, on *Eupomacentrus fasciolatus* (WAM 611-85).

Type locality. Miers (1880) stated that the specimens he examined came from an unlocalised jar of specimens from Bleeker's 'Malaysian' collection. Bleeker's (1857) collection was from Indonesia, not Malaysia, and all but two of the 16 species were recorded from Batavia (= Jakarta). The type locality is here considered to be Java, Indonesia.

Description of female. Body about 1.8 times as long as wide. Cephalon anterior margin truncate, folded ventrally and posteriorly; eyes 0.13–0.22 width of cephalon. Pereonites 1–4 posterolateral angles weakly produced, 5–7 with posterolateral angles more strongly produced. Coxae of pereonite 2 longer than wide. Pereonite 7 posterolateral margins produced to between pleonite 3 and pleonite 5. Pleonites 1–5 posterior margin evenly rounded.

Antennule distinctly longer than antenna, with 7 articles, articles 1–4 conspicuously flattened (articles 6 and 7 partly coalesced in illustrated female); antenna slender, composed of 6–7 articles.

Mandible palp article 3 with 2 short setae. Maxillule with 4 terminal spines. Maxilla medial lobe fused to lateral, each lobe with 2 short spines. Maxilliped article 3 with 3 short recurved spines.

Pereopod 1 basis posterodistal margin carinate, posterodistal angle acute, weakly produced; dactylus longer than combined length of merus, carpus and propodus, abruptly recurved two thirds along its length with weak nodule at point of

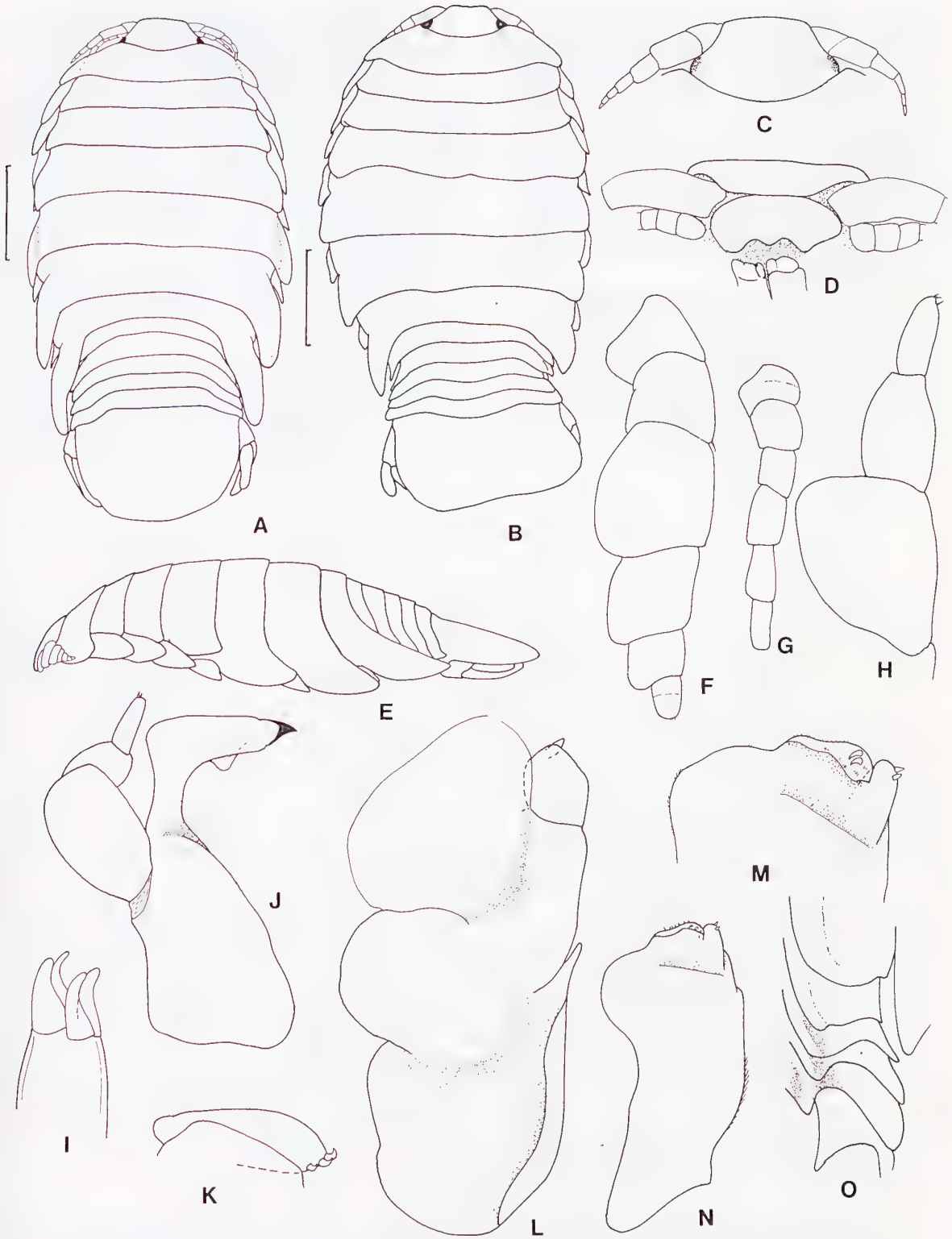

Fig. 2. *Renocila ovata.* A, C–E, lectotype; remainder female, WAM 612-85. **A,** dorsal view; **B,** dorsal view; **C,** cephalon; **D,** frons; **E,** lateral view; **F,** antennule; **G,** antenna; **H,** mandible palp; **I,** maxillule apex; **J,** mandible; **K,** maxilliped article 3; **L,** maxilliped; **M,** maxilla apex; **N,** maxilla; **O,** left pleonites, ventral view. Scale lines represent 4.0 mm.

flexure. Pereopods 2 and 3 similar to 1, basis posterodistal margin more produced on pereopod 2 than on pereopod 1, less produced on pereopod 3, and not produced on pereopod 4. Pereopods 5–7 without carina on basis, without nodule on dactylus; dactylus smoothly curved; pereopod 7 manifestly longer than pereopod 6.

Pleopods all with exopod wider than endopod; proximomedial lobe of endopods 3–5 becoming progressively larger. Uropods short, not extending to posterior margin of pleotelson, endopod about 0.8 length of exopod, both rami broadly rounded, curving medially.

Male. Body about 2.9 times longer than wide; posterolateral margins of pereonites not produced; all pleonites visible in lateral view.

Antennule with 8 articles, longer than antenna, but not as flattened as that of female. Antenna with 8 articles. Mandible with molar process prominent; palp basal article narrow, article 3 with 4 setae. Maxilla medial lobe less distinctly fused, suture partially apparent. Pereopods 1–3 without carina on basis; dactylus smoothly curved, without nodule on anterior margin. Pleopods more elongate than in female. Uropod exopod about 1.7 times longer than endopod; endopod rounded, exopod with acuminate apex.

Colour. Dark slaty brown, appearing nearly black.

Size. Ovigerous females 10.0–25.0 mm, males 7.0, 9.0 mm.

Variation. Posterolateral margins of pereonite 7 may be produced to posterior of pleon, or just reach pleonite 3. Male uropod gradually approaches female form as size increases.

Remarks. *Renocila ovata* is easily identified by the large flattened antennule, abruptly recurved dactylus on pereopods 1–4, broad pleon, and strongly produced posterolateral margins on pereonites 5 and

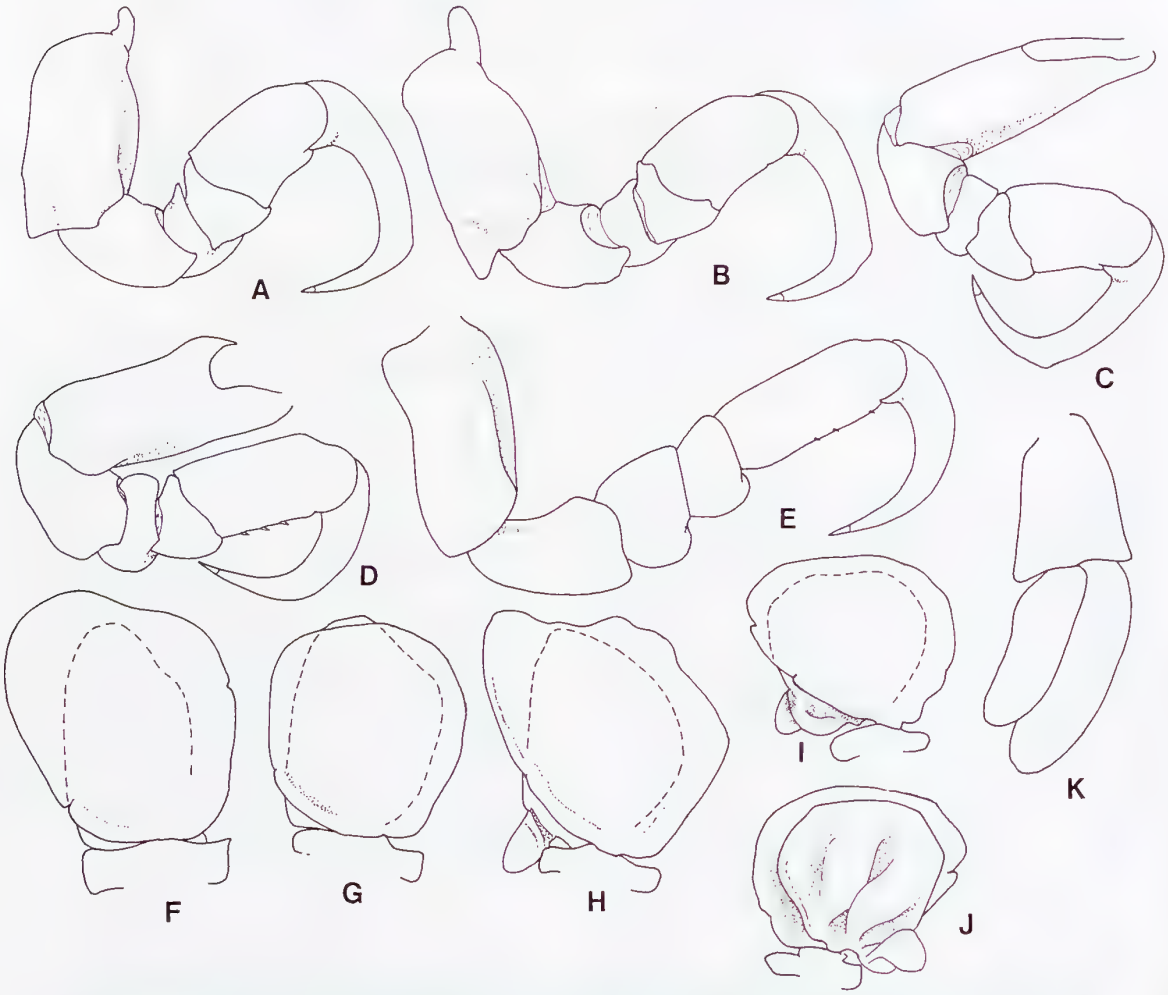

Fig. 3. *Renocila ovata.* All figures female, WAM 612-85. **A,** pereopod 1; **B,** pereopod 2; **C,** pereopod 4; **D,** pereopod 6; **E,** pereopod 7; **F–I,** pleopods 1–3, 5 respectively; **J,** pleopod 5, posterior view; **K,** uropod.

6. *Renocila indica* differs from *R. ovata* in having a more oval body outline, a narrower pleon, pereopods 1–3 basis with crescent posterodistal process, and uropod exopod proportionally much longer.

Examination of the types of *Lironeca dubia* Nierstrasz (1918, 1931) reveal that species to be a junior synonym of *R. ovata.*

Barnard (1936) recorded *Renocila ovata* from India, and gave figures of the maxilliped, mandible palp and pereopods 1 and 7. The figure of pereopod 1 differs from material examined here in having the posterodistal angle of the basis far more strongly produced, the posterior margin of the ischium carinate, and a shorter dactylus without nodules. Pereopod 7 differs by having a prominent carina on both the basis and ischium. Barnard's material is not *Renocila ovata,* but is probably *Renocila alkoo.*

Hosts. Known only from *Eupomacentrus fasciolatus* and an unidentified *Apogon* species. Isopods are situated posterior to the pectoral fin, one on each side of the host.

Distribution. Carnarvon and Point Quobba, WA; several localities in Indonesia.

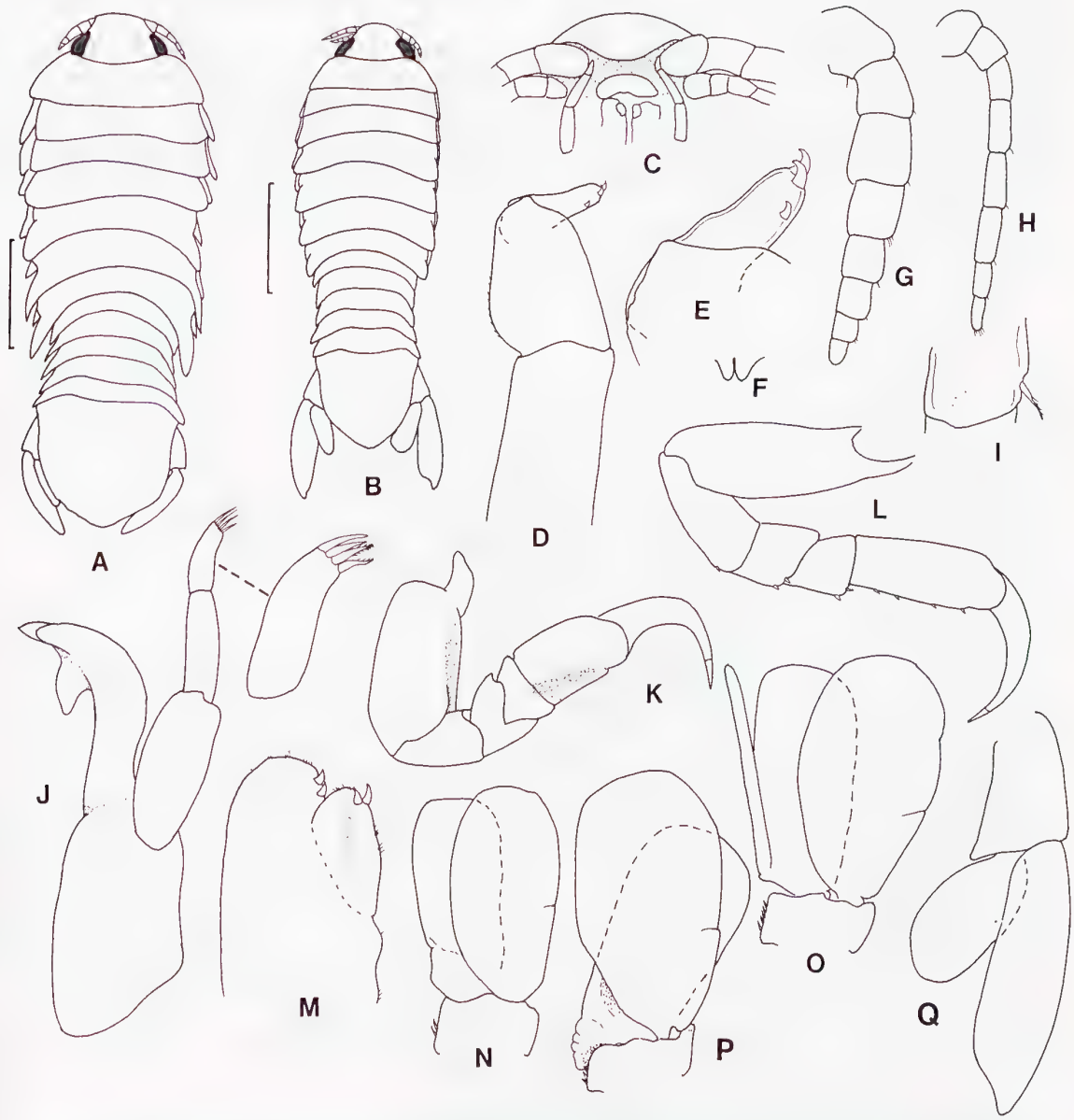

Fig. 4. *Renocila ovata.* **A,** male, north-east Flores (ZMA Is. 105.055), syntype of *Livoneca dubia.* Remainder male, WAM 611-85: **B,** dorsal view; **C,** frons; **D,** maxilliped; **E,** maxilliped article 3; **F,** penes; **G,** antennule; **H,** antenna; **I,** antenna article 4; **J,** mandible; **K,** pereopod 1; **L,** pereopod 7; **M,** maxilla apex; **N–P,** pleopods 1–3 respectively; **Q,** uropod. Scale lines represent 2.0 mm.

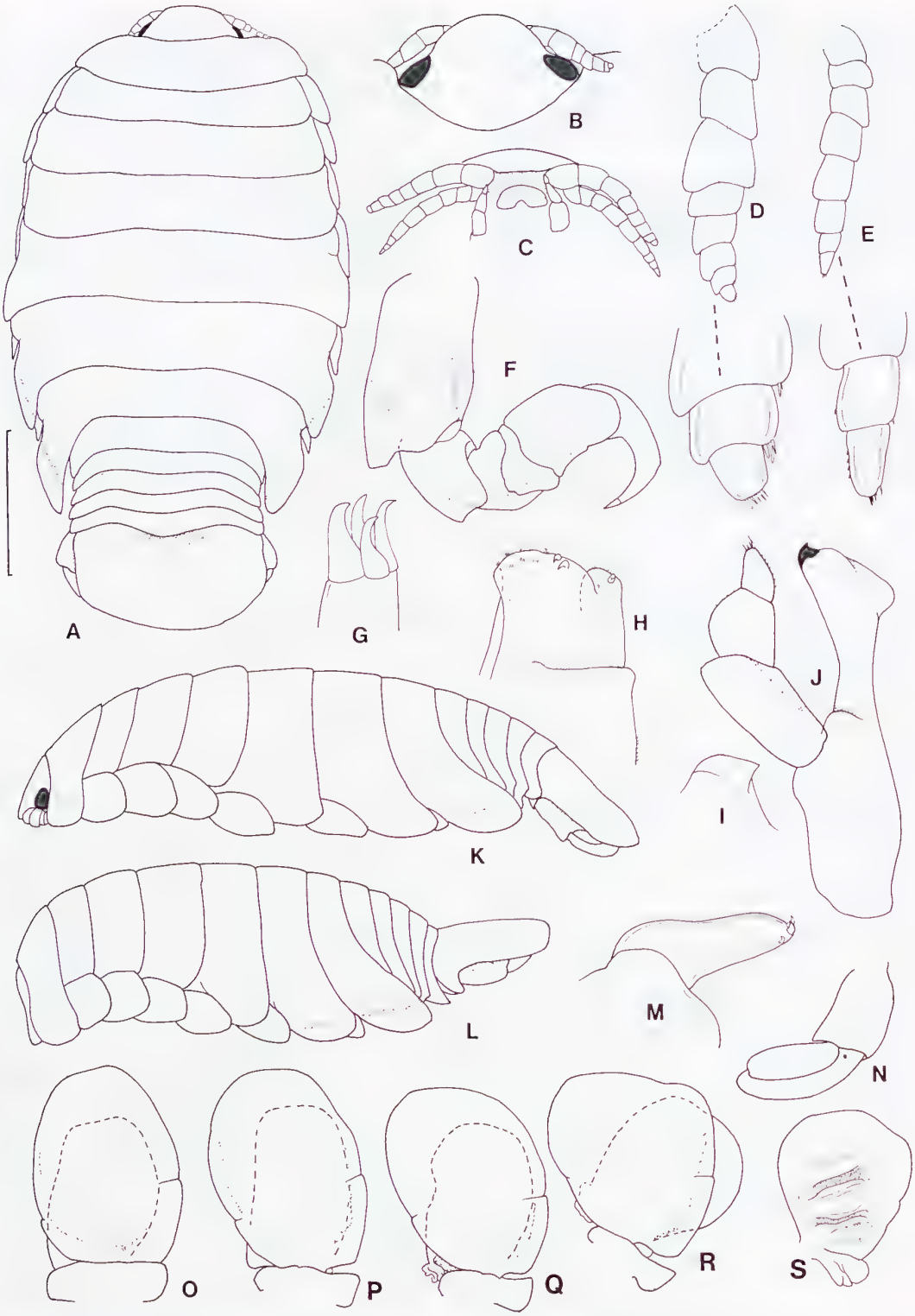

Fig 5. *Renocila alkoo* n. sp. A-K, M, holotype; L, N-S, paratype AM P25008. **A,** dorsal view; **B,** cephalon; **C,** frons; **D,** antennule and detail; **E,** antenna and detail; **F,** pereopod 1; **G,** maxillule apex; **H,** maxilla apex; **I,** right mandible apex; **J,** right mandible; **K,** lateral view; **L,** lateral view; **M,** maxilliped article 3; **N,** uropod; **O–P,** pleopods 1, 2, 3 and 5 respectively; **Q,** pleopod 5 endopod, posterior view. Scale line represents 3.0 mm.

Renocila alkoo n. sp.

Figs 5, 6

? *Renocila ovata*.—Barnard, 1936: 161, fig. 5 (not *R. ovata* Miers, 1880).

Material examined. All Great Barrier Reef, Queensland. HOLOTYPE: female (ovig 13.5), Bushy Is., Redbill Cay, June 1975, from mixed sample of reef flat fish, coll. R.J. McKay (QM W10844). PARATYPES: female (non-ovig 10.5), Gillett Cay, Swains Reefs, 14 Oct 1962, reef flat (AM P37138); female (non-ovig 12.0), One Tree Is., Capricorn Group, 5 Oct 1971, coll. D. Hoese (AM P25008).

Type locality. Bushy Island (Redbill Cay), Great Barrier Reef, 20°57′S, 150°05′E.

Description of female. Body about 1.8 times as long as wide. Cephalon anterior margin smoothly rounded, eyes about 0.26 width of cephalon. Coxae of pereonites 1–2 as wide as long, those of pereonites 4–7 rapidly decreasing in length. Posterolateral margins of pereonites 6–7 weakly produced, laterally bent. Pleon about 0.35 width of pleon, lateral margin subparallel; pleonite 1 longest. Pleotelson lateral margins subparallel, posterior subtruncate.

Antennule extending to pereonite 1, with 8 articles. Antenna slightly shorter than antennule, with 8 articles.

Mandible palp article 3 with 4 terminal setae. Maxillule with 4 terminal spines. Maxilla with 1 or 2 small spines on medial lobe, 2 on lateral lobe. Maxilliped article 3 with 3 recurved spines.

Pereopod 1 basis posterodistal angle carinate, produced, truncate; posterior margins of ischium and merus carinate, carpus indistinctly so; dactylus short, extending to carpus, abruptly curved, anterior margin with very weak nodule. Pereopods 2 and 3 similar to 1 but basis posterodistal angle not as produced, posterior margins of ischium and merus not as obviously carinate. Pereopods 6 and 7 similar in length, both with basis anterolateral margin carinate; pereopod 7 with 3 small spines on propodus palm, 2 on carpus, 1 on ischium.

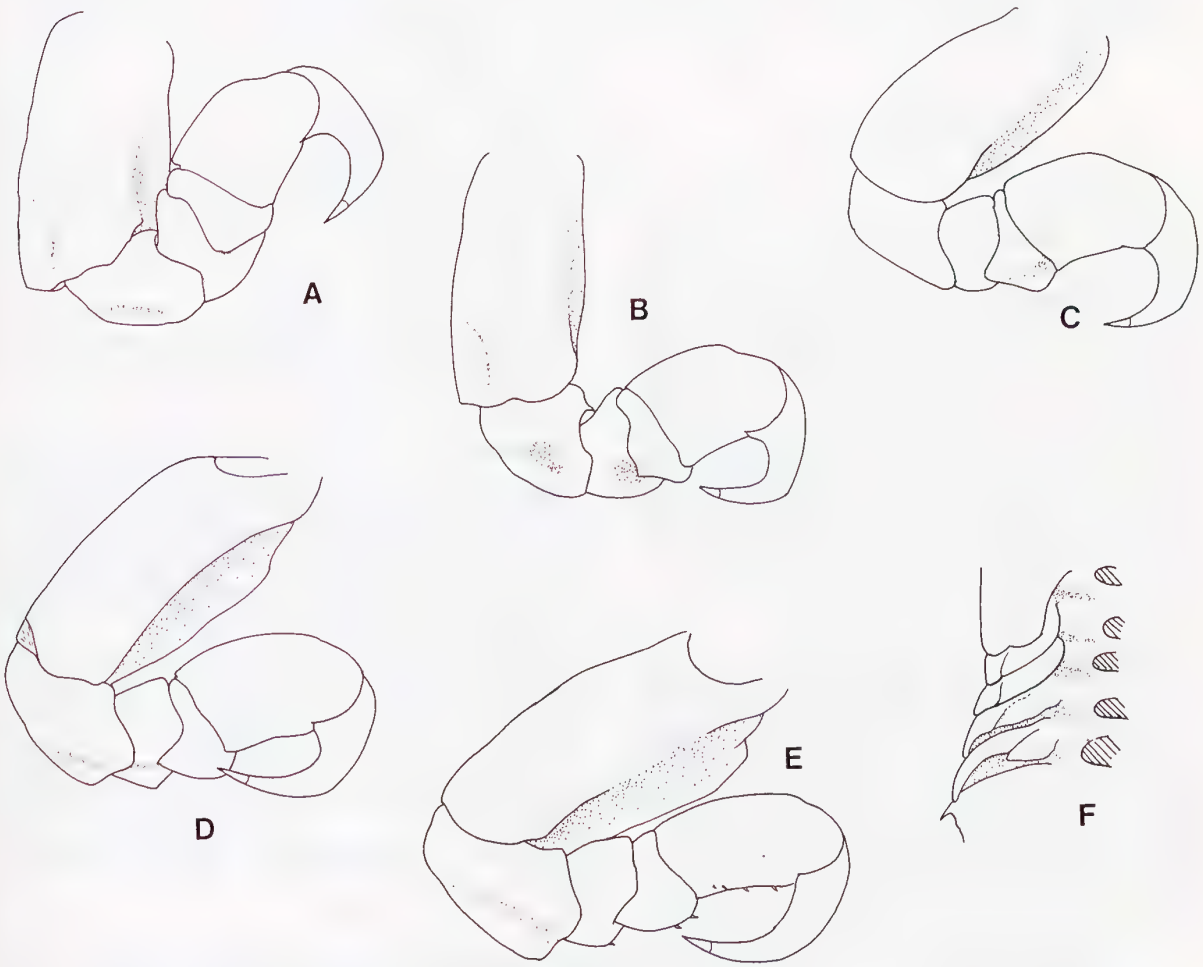

Fig. 6. *Renocila alkoo* n. sp. All figures female, AM P25008. **A–E**, pereopods 1, 2, 4, 6 and 2 respectively; **F**, left pleonites, ventral view.

Pleopod 5 endopod folding weak. Uropod with rami short, broadly rounded, endopod slightly shorter than exopod.

Male. Not known.

Colour. In alcohol, dark grey.

Size. Ovigerous female, 13.5 mm, non-ovigerous 10.5–12.0 mm.

Variation. The female from One Tree Island is far more strongly arched, and the cephalon is scarcely visible in dorsal view. Only the holotype has the posterodistal angle of the basis produced.

Remarks. This species bears some resemblance to *Renocila ovata* but is easily distinguished by having far shorter pereopod dactylus, longer antenna, pereopod 7 manifestly larger than 6 (both with a weakly carinate basis), and posterodistal angle of pereopod 1 basis truncate.

Hosts. None recorded.

Distribution. Great Barrier Reef from the Capricorn Group in the south to Swains Reefs and Bushy Island reef off Mackay.

Etymology. *Alkoo* is an Aboriginal word meaning visitor.

Renocila plesiopi n. sp.

Figs 7, 8

Rocinela species.—Healy & Yaldwyn, 1970: 26, pl. 11 (lapsus).

Material examined. All Great Barrier Reef, Queensland. HOLOTYPE: female (ovig 19.0), Gillett Cay, Swains Reefs, 14 Oct 1962, ex *Plesiops corallicola* (AM P37139). PARATYPES: 2 females (ovig 13.5, non-ovig 13.5), same data as holotype (AM P15598); female (12.0), on host, photographed by Healy & Yaldwyn, 1970 (AM P15597); female (ovig 10.0), no host (AM P15600); female (ovig 8.5), Gillett Cay, Swains Reefs, 14 Oct 1962, ex *Apogon* sp. (AM P15599); female (ovig 13.5), Heron Island, Capricorn Group, 23°27′S, 151°55′E, Sept 1926, caudal peduncle of *Apogon guttatus*, coll. M. Ward (AM P10686); female (non-ovig 12.5), One Tree Is., Capricorn Group, 23°30′S, 152°05′E, 29 Sept 1971, west channel, sand and coral bottom, coll. D. Hoese & V. Moore (AM P25006).

Type locality. Gillett Cay, Swains Reefs, Great Barrier Reef, 21°43′S, 152°25′E.

Description of female. Body about 1.6 times as long as wide; widest at pereonite 5. Cephalon rostrum anterior margin turned ventrally and posteriorly; eyes small, about 0.28 width of cephalon. Coxae of pereonites 2–3 as long, or slightly longer than respective segment; coxae of pereonites 5–6 short, coxae of pereonite 7 much shorter than 6. Posterolateral margins of pereonites 4–7 produced, acute. Pleonite 1 longest; pleonites 2–4 becoming progressively narrower, pleonite 5 slightly wider than pleonite 4; pleon (at pleonite 4) about 0.35 width of pereon. Pleotelson wider than long, posterior margin widely rounded.

Antennule extending to midpoint of pereonite 1, with 7 articles. Antenna slightly shorter than antennule, with 9 articles.

Mandible palp article 3 with 7 setae. Maxillule with 5 terminal spines. Maxilla with 2 small spines each on medial and lateral lobe respectively. Maxilliped article 3 with 4 small tubercle-like spines.

Pereopod 1 basis posterodistal margin carinate; dactylus without nodules, curving smoothly, extending to posterior of ischium. Pereopods 2 and 3 similar to 1 but slightly longer; pereopod 4 basis longer than in pereopod 3, posterodistal angle not carinate. Pereopod 6 with 4 short spines on propodial palm, dactylus manifestly shorter than those of anterior pereopods. Pereopod 7 slightly longer than 6; merus, carpus and propodus proportionally longer than in pereopod 6.

Pleopods 3–5 endopod proximomedial lobe slender; peduncles decreasing in width towards posterior. Uropod endopod straight, tapering to narrowly rounded apex; exopod curving medially, apex rounded.

Male. Not known.

Colour. All specimens with submarginal band of chromatophores along posterior margin of pereonites 2–7, and both anterior and posterior margins of pereonite 7. A colour photograph was given by Healy & Yaldwyn (1970).

Size. Ovigerous females, 8.5–19.0 mm, non-ovigerous females 12.5 mm.

Variation. Non-ovigerous female maxilliped article 3 with 3 recurved spines. Antenna articles vary in number from 8 to 9. Specimens otherwise constant in appearance.

Remarks. *Renocila plesiopi* is easily separated from all other species by the narrow pleon, which decreases in width towards the posterior. Other characters which aid in identifying the species are the long, smoothly curved dactylus, totally lacking nodules, and the posterodistal margin of the basis of pereopods 1–3 not being produced.

Hosts. *Plesiops corallicola, Apogon* sp. and unconfirmed *Apogon guttatus.* All specimens positioned midway between ventral fin and second dorsal, anterior to the caudal peduncle.

Distribution. Heron Island Reef, One Tree Island reef, Capricorn Group, and Gillett Cay, Swains Reefs.

Etymology. Specific epithet is derived from the host genus name.

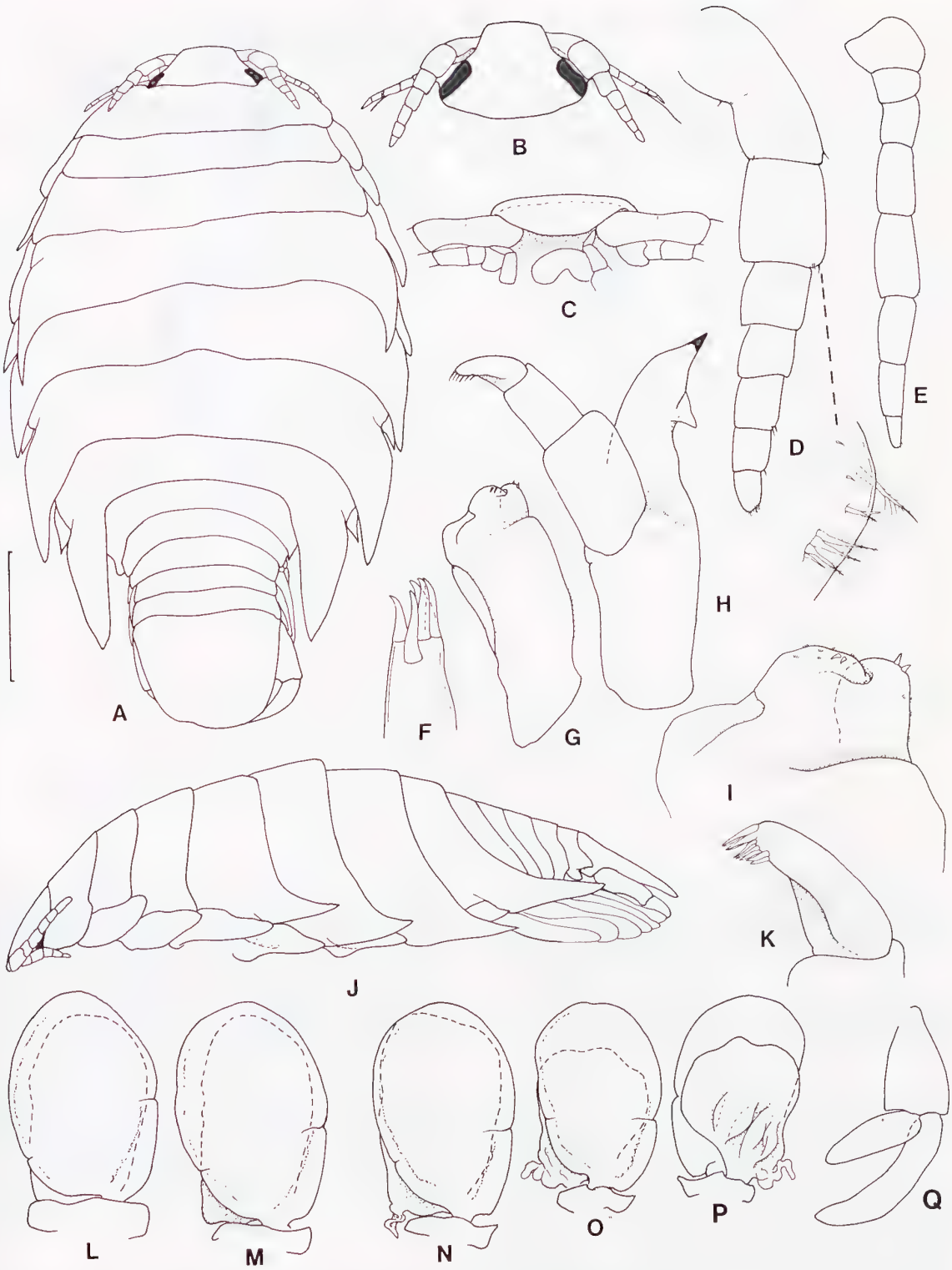

Fig. 7. *Renocila plesiopi* n. sp. A–C, J, holotype, AM P37139; remainder female, AM P15598. **A,** dorsal view; **B,** cephalon; **C,** frons; **D,** antennule, female; **E,** antenna, female; **F,** maxillule apex; **G,** maxilla; **H,** mandible; **I,** maxilla apex; **J,** lateral view; **K,** mandible palp article 3; **L–O,** pleopods 1, 2, 3 and 5 respectively; **P,** pleopod 5, posterior view; **Q,** uropod. Scale line represents 4.0 mm.

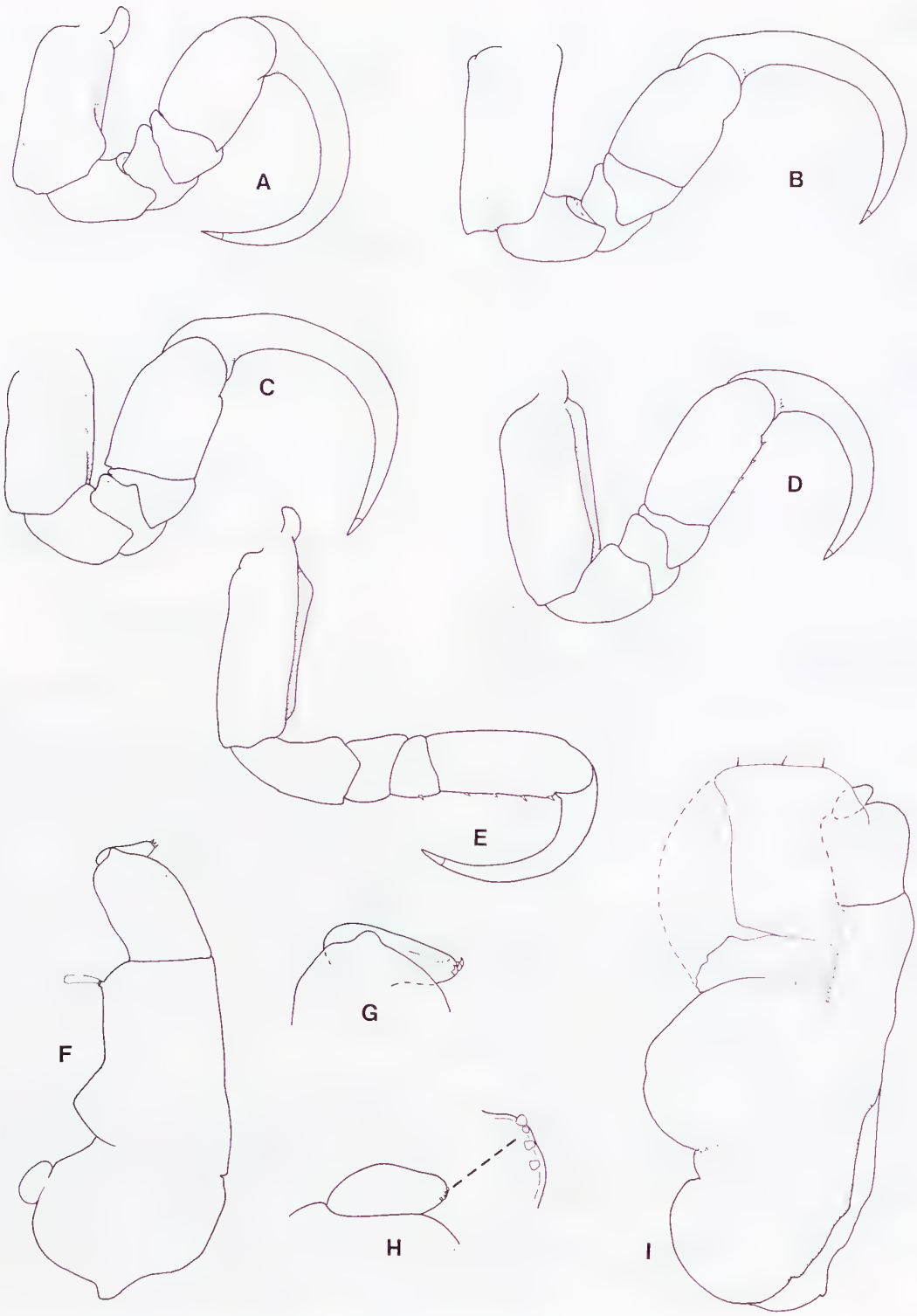

Fig. 8. *Renocila plesiopi* n. sp. All figures of female, AM P15598, except where indicated. **A–E,** pereopods 1, 2, 4, 6 and 7 respectively; **F,** maxilliped, non-ovig female, AM P25598; **G,** maxilliped article 3, non-ovig female, AM P15598; **H,** maxilliped apex; **I,** maxilliped.

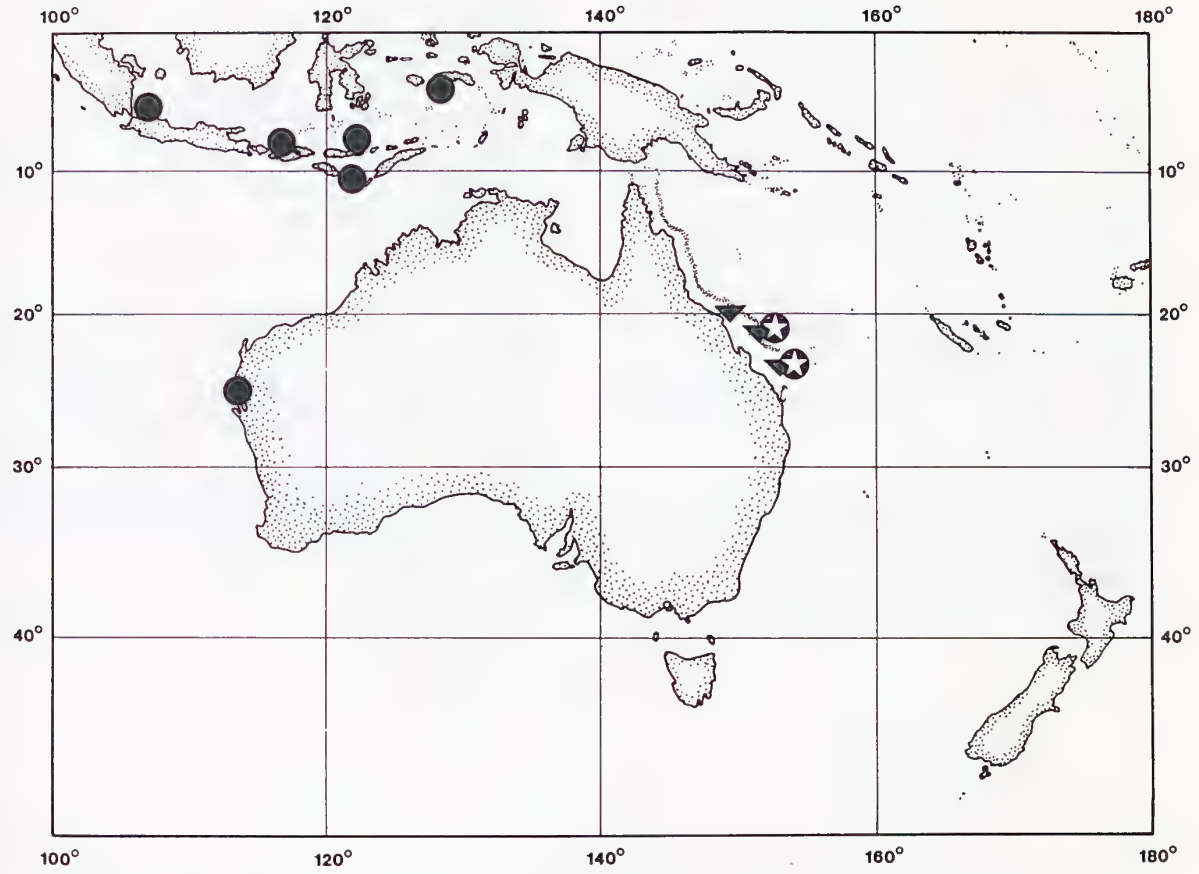

Fig 9. Distribution of *Renocila* around Australia, and Indonesia: *R. ovata,* circle; *R. alkoo,* triangle; *R. plesiopi,* star in circle.

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References

Barnard, K.H., 1936. Isopods collected by R.I.M.S. *Investigator.* Records of the Indian Museum, Calcutta 38: 147–191.

Bleeker, P., 1857. Recherches sur les Crustacés de L'Inde Archipelagique. II. Sur les Isopodes Cymothoadiens de L'Archipel Indien. Natuurkundige vereeniging in Nederlandsche-Indie, Batavia. Verhandelingen 2: 20–40, plates 1, 2.

Bowman, T.E. & R.N. Mariscal, 1968. *Renocila heterozota,* a new cymothoid isopod, with notes on its host, the anemone fish, *Amphiprion akalliopisos,* in the Seychelles. Crustaceana 14: 97–104.

Bruce, N.L., 1987. Australian *Pleopodias* Richardson, 1910 and *Anilocra* Leach, 1818 (Isopoda: Cymothoidae), crustacean parasites of marine fishes. Records of the Australian Museum 39: 85–130.

Brusca, R.C., 1981. A monograph on the Isopoda Cymothoidae (Crustacea) of the eastern Pacific. Zoological Journal of the Linnean Society 73: 117–199.

Gerstaecker, A., 1882. Sechste Ordnung. Isopoda Asseln [Part], pp. 97–278 in "Klassen und Ordnung des Thier-Reichs, wissenschaftlich dargestellt in Wort und Bild." (Dr H.G. Bronn ed.). Funfter Band II. Abtheilung. Gliederfüssler: Arthropoda. Crustacea (Zweite Hälfte: Malacostraca) 4, 5, 6, 7, 8. Leiferung.

Healy, A. & J.C. Yaldwyn, 1970. Australian Crustaceans in Colour. A.H. & A.W. Reed, Sydney, 112 pp.

Miers, E. J., 1880. On a collection of Crustacea from the Malaysian Region — Part IV. Penaeidae, Stomatopoda, Isopoda, Suctoria, and Xiphosura. Annals and Magazine of Natural History, 5 series 5: 457–467.

Nierstrasz, H.F., 1915. Die Isopoden-Sammlung im Naturhistorischen Reichsmuseum zu Leiden. — 1. Cymothoidae. Zoologische Mededeelingen, Rijksmuseum van Natuurlijke Historie te Leiden 1: 71–108, plates 3, 4.

_____ 1918. Alte und neue Isopoden. Zoologische Mededeelingen, Rijksmuseum van Natuurlijke Historie te Leiden, 4: 103–142, plates 9, 10.

_____ 1931. Die Isopoden der Siboga-Expedition. 3. Isopoda Genuina. 2. Flabellifera. Siboga-Expeditie 32c: 123–233, plates 10, 11.

Richardson, H., 1910. Marine isopods collected in the Philippines by U.S. Fisheries steamer *Albatross* in 1907–1908. Department of Commerce and Labor, Bureau of Fisheries Document 736: 1–44.

Schiödte, J.A. & Fr. Meinert, 1884. Symbolae ad monographium cymothoarum crustaceorum isopodum familiae. IV. Cymothoidae Trib. II. Cymothoinae. Trib. III. Lironecinae. Naturhistorisk Tidsskrift Series III, 14: 221–454, plates 6–13.

Stebbing, T.R.R., 1900. On Crustacea brought by Dr. Willey from the South Seas in "Zoological results based on material from New Britain, New Guinea, Loyalty Islands, and elsewhere, collected during the years of 1895, 1896 and 1897." (A. Willey ed.) 5(33): 605–690. University Press, Cambridge.

_____ 1924. Crustacea of Natal. Fisheries and Marine Biological Report No. 3, for the year 1922, 3: 1–15, Plates 11–16.

Trilles, J.-P., 1979. Les Cymothoidae (Isopoda, Flabellifera; parasites de poissons) du Rijksmuseum van Natuurlijke Histoire de Leiden II. Afrique, Amérique et régions Indo-Ouest-Pacifiques. Zoologische Mededelingen, Rijksmuseum van Natuurlijke Histoire te Leiden 54: 245–275

Williams, E.H. Jr. & L.B. Williams, 1980. Four new species of *Renocila* (Isopoda: Cymothoidae), the first reported from the New World. Proceedings of the Biological Society of Washington 93: 573–592.

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A New Species of *Phalanger* (Phalangeridae: Marsupialia) from Montane Western Papua New Guinea

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ABSTRACT. *Phalanger matanim* n.sp. is a plesiomorphic species of *Phalanger,* thus far known from only three specimens taken in the Telefomin area at altitudes between 1,550 and 2,600 m. Retention of a well-developed preparacrista on M2/, the presence of small simple molars, and having the periotic visible on the external basicranium in *P. matanim* are plesiomorphic features not otherwise seen in combination in the genus *Phalanger.* Although convergent with the other montane *Phalanger* species *(P. vestitus, P. carmelitae* and *P. interpositus)* in several external morphological features, *P. matanim* does not appear to be closely related to this group. At the upper limit of its altitudinal range, *Phalanger matanim* is sympatric with *P. vestitus* and *S. leucippus,* and at the lower end with these species and also *P. interpositus* and *P. carmelitae.*

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Between 1984 and 1987 the author conducted a survey of the mammals of southern West Sepik Province, Papua New Guinea (Fig. 1). Previously, the mammal fauna of this region was very poorly sampled, and in the course of the work several undescribed species were encountered. This work is intended as the first in a series of publications dealing with the results of this survey. The first specimen of the new *Phalanger* was collected during the 1985 field season, at a locality where four additional phalangerid species *(Strigocuscus leucippus, Phalanger vestitus, P. carmelitae* and *P. interpositus)* occur sympatrically. At first, it was thought that the specimen could have been a hybrid between two of these species, but further research and the discovery of two additional specimens has shown that the material indeed represents a distinct and, until now, undescribed species of *Phalanger.*

The taxonomy of the genus *Phalanger* has, until recently, been in a state of confusion. In the past many forms have been named and then synonymised without close examination. The taxonomy for phalangerid species followed here is that of George (in press), while Flannery *et al.* (in press) is followed for supraspecific groupings.

Materials and Methods

Colours, where capitalised, follow Ridgeway (1886), and dental nomenclature follows Archer (1976, 1978). AM M is the prefix for Australian Museum mammal specimens, CM is the prefix for Australian National Wildlife Collection specimens, DW is the prefix for Papua New Guinea Division of Wildlife mammal specimens (which will ultimately be housed in the PNG Museum), WSP = West Sepik Province, ESP = East Sepik Province, MBP = Milne Bay Province, NP = Northern Province, CP = Central Province, WHP = Western Highlands Province. Measurements were taken using vernier calipers, and weights and measurements were taken on freshly dead specimens in the field. Appendix 1 lists the phalangerid specimens (other than *P. matanim)* examined during this study.

SYSTEMATICS

Phalangeridae, Thomas, 1888
Phalangerinae Thomas, 1888
Phalanger Storr, 1780

Phalanger matanim n.sp.

Figs 2–4, Table 1

Holotype and type locality. AM M14186, puppet skin with skull and dentaries, with P3-M5 erupted, of a subadult male. Collected by T. Flannery, upper Sol River Valley, Telefomin area, West Sepik Province, Papua New Guinea, 5°06′S 141°42′E, 2,600 m, 1 April 1986. Papua New Guinea topographic survey sheet 1-100,000 series, No.7282 (Telefomin, see Fig. 1).

Paratypes. AM M14702, puppet skin and skull of an adult male, collected by T. Flannery, Nong River Valley, 5°11′S 141°35′E, 1,550 m, 9 July 1985, (Fig. 4). DW 8393, puppet skin and skull of adult female, collected by F. Kinbag & L. Seri, Tifalmin, 5°08′S 141°31′E, 1,600–1,800 m, 18 Aug 1984 (Fig. 4).

Etymology. *Matanim* is the Telefol name for this species. This species is named in honour of the people of the Telefomin Valley, whose unceasing goodwill and assistance allowed me to complete my mammal survey of their homeland.

Diagnosis. *Phalanger matanim* n.sp. can be distinguished from all other species of *Phalanger* in possessing the following features: molars smaller and narrower (Figs 2–6); M2/ with well-developed preparacrista that connects with parastyle (occasionally also seen in *P. orientalis);* nasals wedged deeply into frontals in a pattern that is unique within the genus (Figs 2,4); nasals narrower relative to maximum interorbital width than in any other member of the genus (Figs 7-8).

In addition, *P. matanim* differs from its cogeners in the following ways: lacking the spotted pelage, and the anterolingual cingulae of the upper molars as seen in *P. lullulae;* C1/ much shorter than that of *P. orientalis* and the sexes are similarly coloured and similar in size; dorsal stripe broader and more ill-

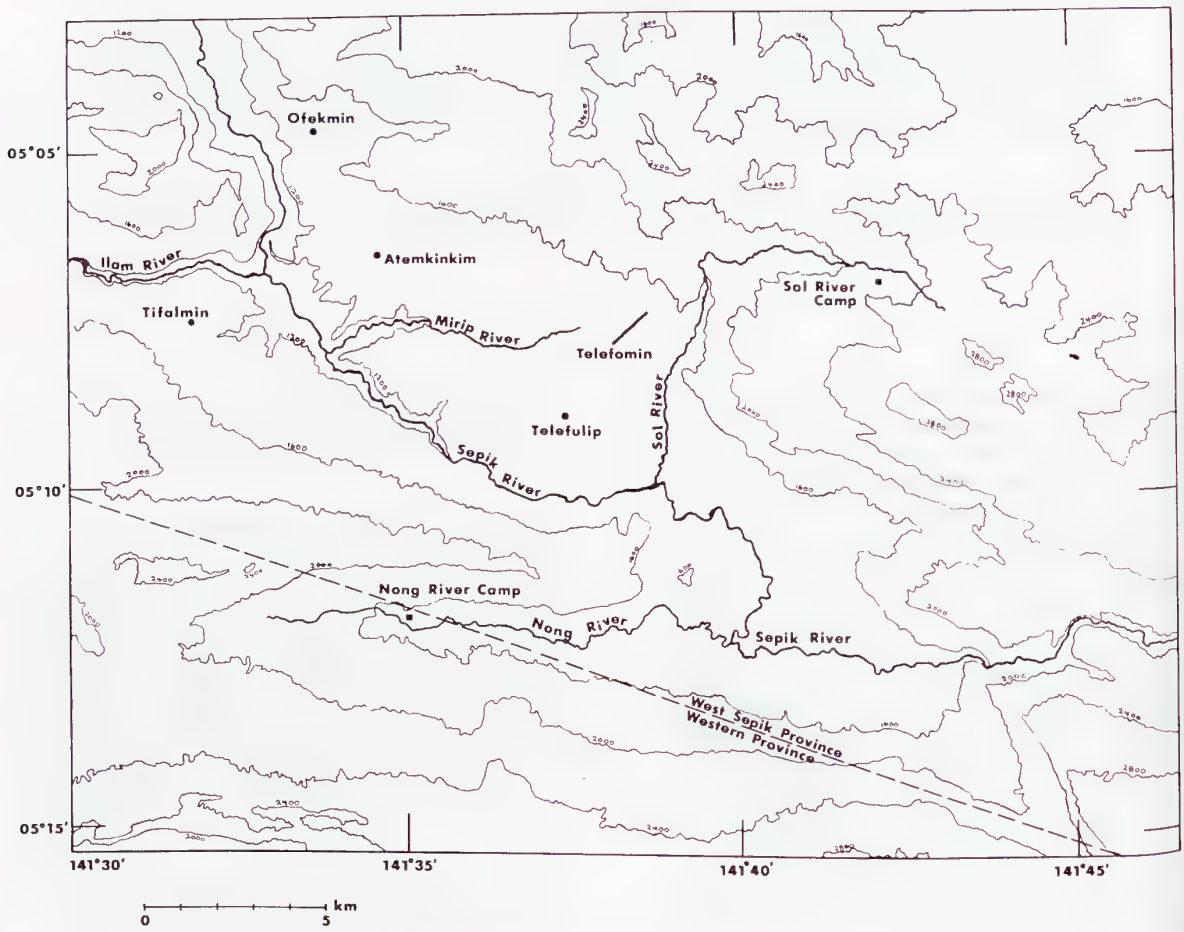

Fig. 1. Map showing the Telefomin Valley and localities where *P. matanim* has been captured.

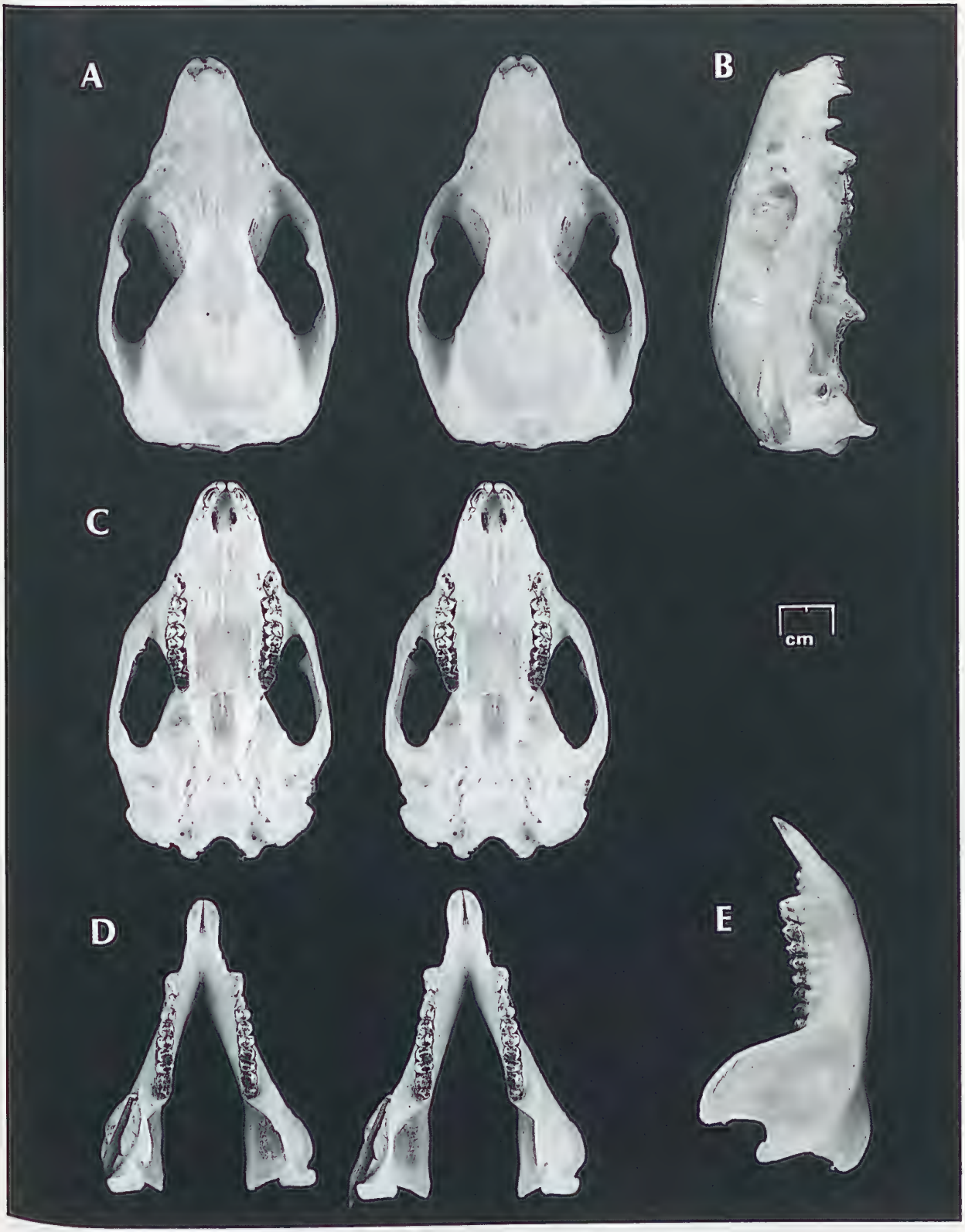

Fig. 2. Skull of the holotype of *Phalanger matanim* (AM M14186) in **A,** dorsal, **B,** ventral (both stereopairs) and **C,** lateral view. **D,** dentary of above in occlusal (stereopair) and **E,** lateral view.

Fig. 3. Puppet skin of the holotype of *Phalanger matanim* (AM M14186) in **A**, dorsal and **B**, ventral views.

defined, and fur longer and laxer than in *P. orientalis;* ears much shorter than those of *P. interpositus* and *P. orientalis;* tail much shorter relative to head-body length than in *P. carmelitae* (see Tables 1–2); external surface of ear almost naked, especially around margin, in strong contrast to densely furred ears of *P. vestitus, P. carmelitae* and *P. interpositus;* greyish colouration and broad dark dorsal stripe differ markedly from black (dorsum) and white (venter) colouration seen in *P. vestitus* and *P. carmelitae;* basal part of naked portion of tail much more strongly tuberculated in male of *P. matanim* than in *P. vestitus* and *P. interpositus.*

Description

Skull and dentition. Skull of holotype has P3/ and M2–5/ erupted but little worn. Thus, although the animal was not sexually mature, full adult dentition was in place.

I1/ projects below level of I2/ to approximately same extent as does C1/, and differs little in morphology from I1/ in other species of *Phalanger.* I2/ subovate in occlusal outline, and much larger than either I1/ or I3/. I3/ tiny with long axis parallel to that of I2/. C1/ short and abuts I3/; similar in morphology to that of other montane *Phalanger* species. I/1 does not differ in morphology from that of other phalangerids.

P1/ short and caniniform; single rooted but has very slight posterior expansion at its base. P2/ miniscule; situated just anterior and slightly medial to P3/. Long axis of P3/ only slightly deflected outwards relative to long axis of molar row; this orientation being closer to that of a species of *Spilocuscus* than *Phalanger;* subovate in occlusal outline; occlusal edge ornamented by three small cuspules. Anterior, buccal and lingual ridgelets extend towards crown base from anteriormost cuspule, and much shorter buccal and lingual ridgelets extend likewise from the more posteriorly positioned cuspules. Posterolingual face of P3/ planar; sharply delimited from lingual face by a ridge. Posterior portion of occlusal edge slopes towards M2/.

Three evenly spaced, tiny peg-like teeth between I/1 and P/3; anteriormost largest, middle one smallest. Orientation of P/3 as in P3/, but tooth less bulbous than P3/. Three small cuspules ornament occlusal crest, anteriormost tallest with buccal, anterior and lingual ridgelets extending towards crown base from this cuspule. Occlusal crest of tooth slopes gently towards crown base posteriorly.

M2/ a simple, narrow tooth, with very few crenulations. Parastyle of moderate size, connecting to well-developed preparacrista, such as seen in ailuropines and trichosurins. Protoloph divided by a fissure placed just lingual to protocone. Several ridgelets and cuspules visible between this structure and paracone. Midlink interrupted at its lowest point by a fissure. It is a simple structure, arising from protocone and hypocone apices, the two sections almost meeting in the interloph valley slightly buccal of these conids. Slight kink, suggestive of presence of reduced stylar cusp, in posterior end of postparacrista, and larger stylar cusp immediately posterior to this, blocking buccal end of interloph valley. Slight bulge in premetacrista suggests presence of a third stylar cusp. Hypoloph better developed than protoloph, and is uninterrupted by fissures. Posterior cingulum U-shaped, composed of well-developed posthypocrista and weaker postmetacrista. No evidence of stylar cusp posterior to metacone, a structure usually present in *Phalanger* species. Lophs subequal in width.

M3/ differs from M2/ in the following ways: parastyle and all suggestions of stylar cusps absent; preparacrista forms much broader arc, enclosing U-shaped basin similar in morphology to that enclosed by posterior cingulum; protoloph slightly wider than hypoloph.

M4/ differs from M3/ in the following ways: smaller, hypoloph relatively narrower, and basin enclosed by posterior cingulum deeper.

M5/ differs from M4/ in the following ways: no hypoloph, and protoloph poorly developed; small cingulum present at base of posterolingual corner of tooth; M5/ much smaller than M4/; posterior moiety relatively narrower.

M/2 of *P. matanim* a narrow, elongate tooth. Trigonid in particular extremely narrow. Paracristid straight and elongate. Slight change in slope in its anterior section suggests the presence of a paraconid. Poorly developed and lower metaconid lingual to tall protoconid. No sign of protostylid, although slight groove on rear face of trigonid present where the protostylid is separated from the protoconid in other phalangerid species. Cristid obliqua poorly developed with only slight suggestion of a kink anterior to hypoconid. Posterior cingulum encloses a U-shaped basin.

M/3 differs from M/2 in protolophid well developed and similar in shape to the hypolophid; the following ways: no paraconid. Protolophid interrupted in its middle by a fissure. Kink in cristid obliqua much better developed.

M/4 very similar in morphology and size to M/3.

M/4 smaller and has hypolophid and protolophid less well developed than M/5.

Skull of the holotype is of a young animal and most sutures are readily visible. Anterior palatal foramena small, extending from just anterior of I3/ to just posterior to C1/. Posterior palatal foramena large in contrast, extending from level with posterior of M2/ to posterior of M5/. Nasals narrow; no nasal lachrymal contact. Posteriorly, nasals

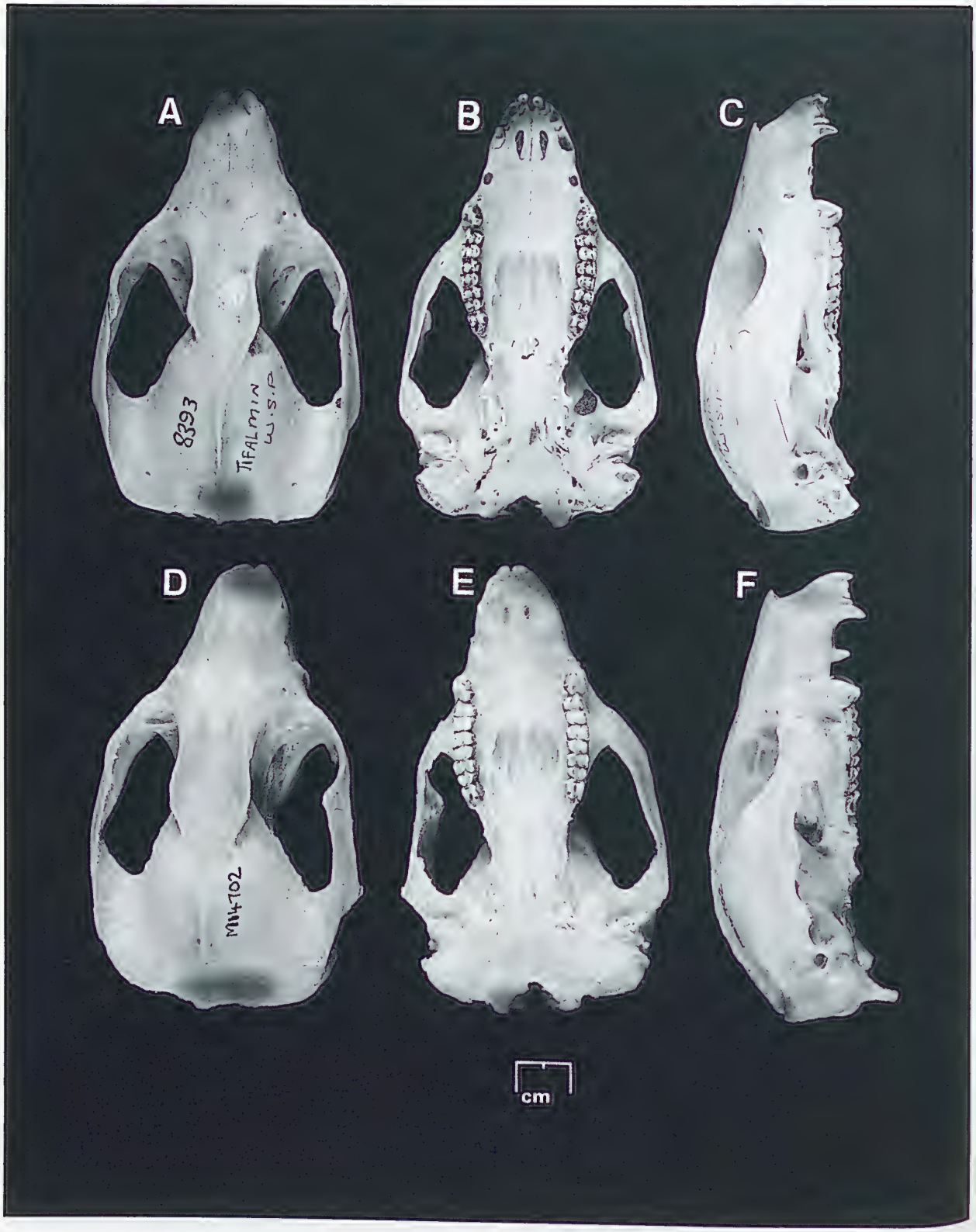

Fig. 4. Skulls of paratypes of *P. matanim*. **A,** AM M14702 in dorsal view, **B,** in occlusal view and **C,** in lateral view. **D,** DW8393 in occlusal view, **E,** in dorsal view, and **F,** in lateral view.

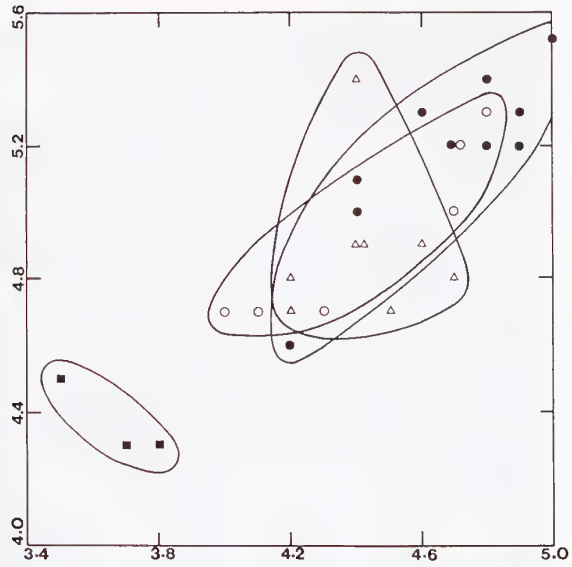

Fig. 5. Bivariate plot of M4/ length (vertical axis) against M4/ width (horizontal axis) in mm for *Phalanger matanim* (square) *P. vestitus* (filled circle) *P. carmelitae* (open circle) and *P. interpositus* (triangle).

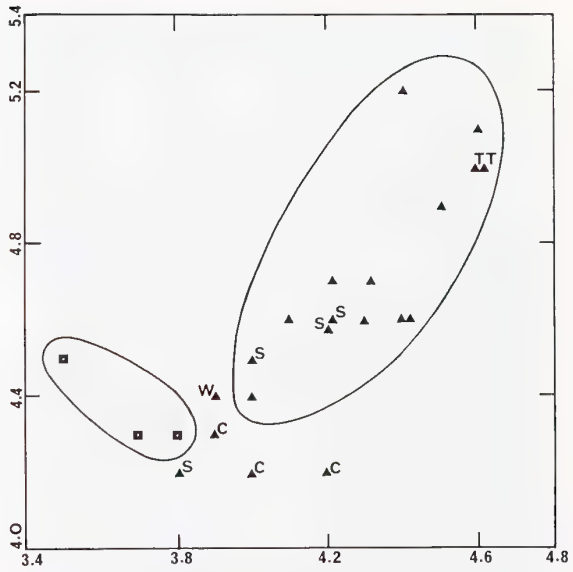

Fig. 6. Bivariate plot of M4/ length (vertical axis) against M4/ width (horizontal axis) for *P. matanim* (square) and *P. orientalis* (triangle). Unlabelled triangles (within ellipse) are specimens from West Sepik Province, c = specimens from Cape York, s = specimens from Solomon Islands, t = specimens from Timor, w = specimens from Wokeo Island (Schouten Group).

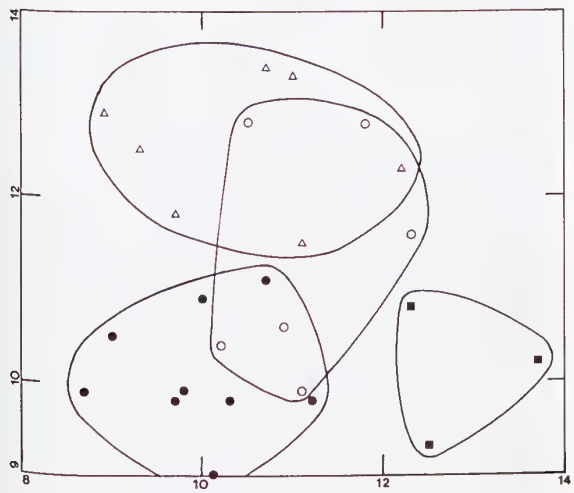

Fig. 7. Bivariate plot of maximum interorbital width opposite the high point of the jugal (vertical axis) against maximum nasal width for *P. matanim*, (squares) *P. vestitus*, (filled circle) *P. carmelitae* (open circle) and *P. interpositus* (triangle).

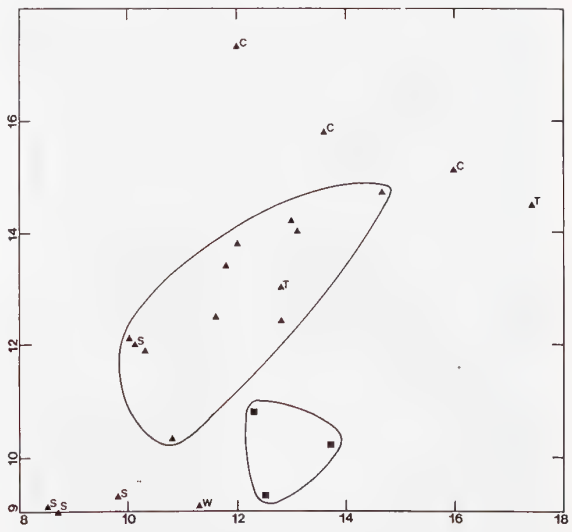

Fig. 8. Bivariate plot of maximum interorbital width opposite the high point of the jugal (vertical axis) against maximum nasal width for *P. matanim* and *P. orientalis* (letters and symbols as in Fig. 6).

wedge deeply into frontals; no noticeable immediate narrowing of nasals where they contact frontals in adults, although some narrowing evident in subadult holotype. In interorbital region, frontals wide (Figs 7–8), reaching their widest point just medial to highest point on jugal. Lachrymal extends well onto face. Maxillary contribution to orbit is low. Ectotympanic contributes to rear face of glenoid fossa along its ventral edge. Mastoid contribution to rear face of cranium restricted to ventrolateral corners of this surface. Alisphenoid roofs the bulla. Sagittal crest not developed. Suprazygomatic foramen large. Paroccipital processes of moderate length. Dentary as in other phalangerids, but small and relatively delicate.

A number of features present on paratype skulls are not apparent on holotype. Skulls of paratypes are from much older animals (both sexually mature) than holotype. The teeth are worn and so do not contribute any additional information. In both specimens, the nasals wedge far more deeply and evenly into the frontals than in the holotype. A low sagittal crest also developed. Both of these features are probably a function of age. Ectotympanic-squamosal suture on postglenoid process difficult to see on paratypes, but it seems that in these specimens the ectotympanic makes up only the ventral-most lip of this structure, whereas it is more extensive dorsally in the holotype. The morphology of this feature could also be a function of age (see Flannery *et al.* in press).

External morphology. The overall colour pattern in all three specimens of *Phalanger matanim* is as follows: various shades of grey on the dorsal surface with black- and silver-tipped guard hairs, a broad and dark dorsal stripe (extending from anterior to and between the eyes anteriorly to a level on the dorsal surface equivalent to the cloaca posteriorly), and a pure white venter. Overall the fur is dense and luxurious, being more similar in texture to that of *Phalanger vestitus* than *P. orientalis*. In the adult male the underfur of the dorsal surface is Smoke Grey, while in the female and subadult male the colour is Drab Grey. The black- and silver-tipped guard hairs give a grizzled appearance to the coat. Black-tipped guard hairs are less frequent on the adult male than in the other specimens. The white fur on the ventral surface extends to within 2–3 cm of the lower lip anteriorly and to within 1 cm of the cloaca posteriorly on all specimens. The white fur extends onto the base of the limbs, but not onto the elbow as is common in *P. interpositus*. The scrotum is white in the males, and in the female the pouch is surrounded by Russet hairs. One nipple is enlarged in the pouch of the female. The fur at the tip of the hairy tail is Seal Brown in the female, the same colour as the dorsal coat in the adult male, while the entire tail is Black in the subadult male. There is no suggestion of a white ear flash on any specimen. The rim of the short ear is very thinly furred. The feet are well furred except on the hallux and distal phalanges, and the hands lack fur on the phalanges. Overall the feet and hands are slightly lighter in colour than the dorsal surface, and in the adult male in life the limbs had a yellowish tinge. This is not obvious on the study skin. The naked skin of the tail in the two males is heavily tuberculated in its ventroproximal portion. In the female the tubercles are barely raised. The distal one half to two thirds of the naked part of the tail is white. All vibrissae are black, and a slight dark eye ring is visible on the subadult male and female.

Overall, the adult male is the lightest specimen, the female a little darker and the subadult darkest. *Phalanger matanim* may therefore lighten with age. The slight constriction of the white underfur visible on the holotype is the result of taxidermy.

Discussion

Systematics. Initially it appeared possible that *P. matanim* may have been related to the poorly-known type specimens of either *P. vestitus* or *P. interpositus*. Mr James Menzies kindly made measurements of these types available to me and it was at once apparent that *P. matanim* differs greatly from them. In M2–5/ length and P3/ width *P. matanim* is much smaller than any of the type series of *P. interpositus* and is clearly distinct from them. (*P. matanim:* M2–5/L;$\bar{x}$=18.6, R=18.1–19.0, N=3; P3/W; $\bar{x}$=3.7, R=3.6–3.8, N=3. *P. interpositus* type series M2–5/L; $\bar{x}$=20.6, R=20.2–20.7, N=4; P3/W; $\bar{x}$=4.2, R=4.0–4.3, N=4). The type of *P. vestitus* is a juvenile but M2–3/ length (the only measurement available) is 10.8, larger than it is for *P. matanim* $\bar{x}$=10.0, R=9.8–10.2, N=3).

The precise relationships of *Phalanger matanim* are as yet uncertain and their determination depends to some extent on a comprehensive revision of the interrelationships of all phalangerins. At higher levels, though, some precise statements concerning relationships can be made. *Phalanger matanim* is certainly a phalangerine, as it possesses all 10 synapomorphies listed for the subfamily in Flannery *et al.* (in press), including restriction of the mastoid to the ventral edge of the rear face of the cranium, and presence of an orbital wing of the maxilla. It is also certain that *P. matanim* is not a trichosurin, as it lacks all of the synapomorphies of that tribe (Flannery *et al.*, in press). These data suggest a relationship with the Phalangerini, but *P. matanim* possesses few of the synapomorphies for this group. Of the five phalangerin synapomorphies listed in Flannery *et al.* in press, only one (loss of C1/–I3/ diastema) is present in *P. matanim*. The others (enlargement of the orbital wing of the maxilla, possession of complexly crenulate molars, obscuring of the periotic by alisphenoid/basoccipital fusion, and

reduction of the strength of the M2/ preparacrista) are not seen in this species. However, a further feature, considered a synapomorphy for the genus *Phalanger* (extreme I3/ reduction) is present in *P. matanim*. Clearly a revision of phalangerin relationships is desirable, but such a study is beyond the scope of the present work.

Within the Phalangerini, *Phalanger matanim* shares features with both species of *Spilocuscus* and *Phalanger*. The shape of the nasal-frontal suture in *P. matanim* and *Spilocuscus* species is remarkably similar, and is not seen elsewhere within *Phalanger*. The presence of a dorsal stripe, and extremely reduced I3/, however are features seen in *Phalanger* species but not *Spilocuscus*. The pupil shape in both of these genera is distinctive, so it is particularly unfortunate that the pupil shape in *P. matanim* is not known. At present *P. matanim* is placed in the genus *Phalanger*, as much because of overall similarity as because of the few synapomorphies that suggest this. This is because the cladistic evidence is equivocal. If the species is thus correctly placed, there has been much more convergence during phalangerid evolution than has been previously recognised. This would include the independent acquisition of the four phalangerin synapomorphies not seen in *P. matanim* in the species of *Spilocuscus* and remaining *Phalanger*. Alternatively, reversion to the plesiomorphic state could have occurred in these four features in *P. matanim*, although this seems unlikely. A third possibility, however, exists. *Phalanger matanim* could be a survivor of a lineage that split from the phalangerin line before *Spilocuscus* and *Phalanger* differentiated. This would require convergence in only one feature (extreme reduction in I3/) between the other species of *Phalanger* and *P. matanim)*. However, if this is correct, a new genus would need to be erected for *matanim*, a move that I feel is unjustified given the present uncertainty regarding phalangerid interrelationships.

It is clear that *Phalanger matanim* is convergent on the montane *Phalanger* species *P. vestitus, P. carmelitae* and *P. interpositus* in a number of features. Like these species, it has luxuriant silky fur, and like *P. vestitus* and *P. carmelitae*, has very short ears. The ears are markedly unlike those of these three species, however, in being very thinly furred, almost naked at the rim, as in *P. orientalis* and *S. leucippus*. In the three other montane species the external surface of the ears is densely furred.

Although *P. matanim* superficially resembles *P. orientalis*, many features argue against a close relationship between these forms. These include the broad and ill defined dorsal stripe, a small C1/, lack of sexual dichromatism and sexual size differences in *P. matanim*, and differences in fur texture and ear length. The consistently well-developed preparacrista on M2/ is a further distinguishing feature as it is seen only very occasionally in *P. orientalis*. Indeed, most of the similarities shared between *P. matanim* and *P. orientalis* seem to be symplesiomorphies, e.g. small molars.

Zoogeography. Extensive collections of phalangerids have now been made throughout most parts of Papua New Guinea, and as far as is known, no further examples of *Phalanger matanim* have been found. These data seem to suggest a real absence of this distinctive species from the eastern half of the island of New Guinea. In contrast, the western half of the island of New Guinea has been poorly sampled for phalangers, and it would not be surprising to find that the range of *P. matanim* extends westwards from the Telefomin area into Irian Jaya.

The occurrence of a small-toothed species of *Phalanger* at altitudes in excess of 2,500 m is surprising. The only other phalangerids that occur at such altitudes in the Telefomin area are *P. vestitus* and *S. leucippus*. The latter, however, is rare. This statement of altitudinal distribution probably holds for most of the island of New Guinea (see Zeigler, 1982). At the lower end of its altitudinal range *P. matanim* is sympatric with *P. vestitus, P. carmelitae, P. interpositus* and *S. leucippus*, at least at the Nong River collecting station, south of Telefomin (Fig. 1). Indeed, specimens of all five of these species were taken within a few days at the Nong River camp at 1,500–1,600 m. Slightly below this altitude (1,400–1,500 m) is the uppermost limit of the sixth phalangerid species to inhabit the Telefomin Valley, *Phalanger orientalis*.

Biology. Little has been learned of the diet, habits and reproduction of *Phalanger matanim*. This species is, however, probably the rarest of the *Phalanger* species to occur in the Telefomin area, as extensive collecting there has resulted in the capture of only three specimens; while many individuals of most other species have been taken. The Telefol name for *P. matanim, Matanim*, is shared with a second biological species, *P. carmelitae*. However, when questioned further most Telefol respond that there are two kinds of *Matanim, Tim Matanim* (a black one identified here as *P. carmelitae)* and the 'true *Matanim'*, that is identified here as *P. matanim*. Both species are frequently characterised as having abundant subcutaneous fat.

All that is known of reproduction in *P. matanim* is that a subadult male was collected in March 1986, and a female with one enlarged teat was taken in August 1984.

The holotype of *P. matanim* was reported by the hunter who caught it to have been sleeping in a lair among rocks. Indeed, Telefol in general believe that *Matanim* are most abundant in rocky areas, and that their lairs are more often found among rocks than in tree hollows.

Summary

1) *Phalanger matanim* n.sp. is a rare and plesiomorphic species of *Phalanger,* at present known only from altitudes of 1,550–2,600 m in the Telefomin area of West Sepik Province.

2) This species may be the sister taxon of previously recognised species of *Phalanger (sensu* Flannery *et al.,* in press) or may be derived from an even earlier split during phalangerin evolution.

3) There is some evidence that *P. matanim* nests most often in rocky areas, and at the lower end of its altitudinal range is sympatric with *P. vestitus, P. carmelitae, P. interpositus* and *S. leucippus.*

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NO.	SEX	HB	TV	HB/TV	FW	HF	E	WT	CBL	BZW	MIBW	NL
AM M14186 (Holotype)	♂	344	275	1.25	42.2	40.1	20.0	1,100g	70.6	43.0	12.5	24.5
AM M14702	♂	438	300	1.46	57.5	45.3	21.0	2,000g	77.6	47.4	13.7	29.8
DW8393	♀	410	315	1.30	59.2	41.0	20.6	—	77.3	47.4	12.3	27.3

NO.	SEX	NW	M2-2W	C1-1W	MW	CTL	ML	P3L	P3W	M2L	M2W	M4L	M4W	M5L	M5W
AM M14186	♂	9.3	21.6	12.8	35.9	22.7	18.1	4.8	3.6	5.0	3.7	4.5	3.5	4.1	3.3
AM M14702	♂	10.2	23.5	13.6	40.5	23.3	23.3	5.1	3.6	5.1	3.8	4.3	3.8	4.4	4.3
DW 8393	♀	10.8	24.1	15.2	41.2	23.6	23.6	4.7	3.8	5.2	3.8	4.3	3.7	4.5	3.3

Table 1. Measurements in millimetres and grams for all known specimens of *Phalanger matanim.* **HB** = length of head and body, **TV** = tail length, **HB/TV** = head body–tail vent ratio, **FW** = length of dorsal fur wedge into naked tail, **HF** = hindfoot length (s.u.), **E** = ear length, **WT** = weight, **CBL** = condylobasal length, **BZW** = bizygomatic width, **MIBW** = maximum interorbital width opposite high point of jugal, **NL** = nasal length, **NW** = nasal width, **M2–2W** = M2/-M2/ external width, **C1-1W** = C1/–C1/ external width, **MW** = Bi-mastoid width, **CTL** = P3/–M5/ length, **ML** = M2/–M5/ length, **P3L** = P3/ length, **P3W** = P3/ width, **M2L** = M2/ length, **M2W** = M2/ width, **M4L** = M4/ length, **M4W** = M4/ width, **M5L** = M5/ length, **M5W** = M5/ width.

	CBL	BZW	MIBW	CTL	ML	M^2L	M^2W	M4L	M4W
P. carmelitae									
STD	3.642	1.766	.747	.961	.768	.242	.313	.273	.344
$\bar{x}$	76.3	47.6	11.2	24.4	20.4	5.4	4.4	4.9	4.4
R	71.4-80.9	45.7-50.5	10.4-12.3	23.1-25.7	19.7-21.3	5.2-5.8	4.1-4.7	4.7-5.3	4.0-4.8
N	6	6	6	6	6	6	6	6	6
P. interpositus									
STD	2.883	1.679	1.164	.589	.652	.238	.177	.713	.535
$\bar{x}$	78.6	47.7	10.4	24.4	20.2	5.4	4.5	4.7	4.3
R	72.2-80.6	44.8-49.3	8.9-12.2	23.5-25.2	19.3-21.2	5.0-5.7	4.3-4.7	4.7-5.4	4.2-4.7
N	7	7	7	7	7	8	8	8	8
P. vestitus									
STD	3.534	1.966	1.704	.829	.727	.2875	.888	.253	.268
$\bar{x}$	81.8	50.9	9.2	25.2	21.4	5.7	4.3	5.2	4.7
R	76.2-86.2	48.5-54.8	8.7-10.9	24.0-26.5	20.2-22.2	5.3-6.2	4.0-5.0	4.6-5.5	4.2-5.0
N	10	10	9	10	10	10	10	10	10
P. orientalis									
STD	7.743	3.815	2.766	1.070	.809	.2273	1.044	.299	.247
$\bar{x}$	80.9	53.8	12.3	23.3	19.0	5.1	4.6	4.6	4.2
R	64.2-95.4	48.5-60.7	8.5-17.3	21.2-24.8	17.4-20.3	4.6-5.3	3.7-4.5	4.2-5.2	3.8-4.6
N	19	11	20	9	9	10	10	20	20

Table 2. Measurements for five species of Phalangeridae with abbreviations as in Table 1 except for $\bar{x}$ = mean, **Std** = standard deviation, **R** = range, **N** = number.

R. Attenborough, on which I was an associate investigator. This work was completed at the Australian Museum, Sydney.

My wife Paula must also be thanked for so patiently bearing with my many absences while on field work in New Guinea. Ms K. Lowe took the photographs, and Ms Barbara Duckworth produced the figures.

References

Archer, M., 1976. Phascolarctid origins and the potential of the selenodont molar in the evolution of diprotodont marsupials. Memoirs of the Queensland Museum 17: 367–371.

_____ 1978. The nature of the molar-premolar boundary in marsupials and a reinterpretation of the homology of marsupial cheekteeth. Memoirs of the Queensland Museum 18: 157–164.

Flannery, T., M. Archer & G. Maynes, in press. The phylogenetic relationships of living phalangerids (Phalangeroidea: Marsupialia) with a suggested new taxonomy. **In** "Possums and Opossums, Studies in Evolution" (M. Archer ed.). Royal Zoological Society of New South Wales.

George, G.G., in press. Characterisation of the living species of Cuscus (Marsupialia: Phalangeroidea). **In** "Possums and Opossums, Studies in Evolution" (M. Archer ed.). Royal Zoological Society of New South Wales.

Ridgway, R., 1886. A nomenclature of colours . . . Little, Brown and Co. Boston, 129 pp.

Ziegler, A.C., 1982. An ecological checklist of New Guinea Recent mammals. **In** "Biogeography and Ecology of New Guinea" (J.L. Gressit ed.): 863–894 Junk, The Hague.

APPENDIX

List of specimens used for comparative purposes in this study.

Phalanger carmelitae. DW8397, AM M14699, AM M13516, Telefomin area WSP; AM M12862, Mt Albert Edward, CP; AM M9519 Hagen Ra. M9518, Jimi Va., both WHP.

Phalanger vestitus. AM M12909, AM M12868-9, AM M12855-7, AM M12863, Mt Albert Edward, CP; AM M14696, AM M13630, AM M15329, Telefomin, WSP.

Phalanger interpositus. AM M13517, AM M14699, AM M13479, AM M14703, AM M14701, AM M14700, Telefomin, WSP; CM12234, Opanabu, CM 12355 Agaun, both MBP.

Phalanger orientalis. AM M14694, AM M14697, AM M15325-8, Torricelli Mts, WSP; AM M13473, AM M13647, AM M13668, Yapsiei Area, WSP; CM 787-8, Cape York; AM M9099, Wokeo Id, ESP; AM M4288, Mt Lamington, NP; AM M10857-8 Timor; AM M5588, AM M5753, AM M5578, AM M3680, Solomon Islands.

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A Revision of the Oriental and Australasian *Medetera* (Diptera: Dolichopodidae)

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ABSTRACT. The Oriental and Australasian *Medetera* (Diptera: Dolichopodidae) are revised and 61 species are recognized, 43 of them new, with 27 Oriental, 29 Australasian, and 5 species occurring in both zoogeographical regions. All species are described and figured except *M. adsumpta* Becker, *M. nudicoxa* Becker and *M. longa* Becker, which were not seen. A key is provided for the separation of males.

The following species are newly placed in synonomy: *M. atrata* Van Duzee, *M. cilifemorata* Van Duzee, *M. hawaiiensis* Van Duzee and *M. palmae* Hardy (=*M. grisescens* de Meijere); and *Elongomedetera thoracica* Hollis (= *M. gracilis* Parent). Lectotypes are designated for *M. apicipes* de Meijere, *M. grisescens* de Meijere, *M. longitarsis* de Meijere, *M. minima* de Meijere, *M. olivacea* de Meijere, *M. opaca* de Meijere, *M. platychira* de Meijere, *M. pumila* de Meijere and *M. vivida* Becker. A neotype is designated for *M. femoralis* Becker. *Medetera comes* Hardy and *M. extranea* Becker are regarded as *nomina dubia. Micromorphus vegandris* (Frey) is a new combination for *Medetera vegandris* Frey.

Of particular interest is the secondary segmentation and articulation of the male cercus in the *salomonis* group, unique among Brachycera. Here the cercus has been divided into discrete basal and distal sections, with the distal section freely articulated on basal section.

Three high altitude species from Nepal have relatively long and broad wings. Several species have orientated silvery pruinosity.

A phylogenetic analysis of the major *Medetera* species groups is presented.

The Australasian *Medetera* fauna, although with distinctive elements, is derived from the Oriental fauna. The Pacific Ocean has progressively fewer species moving eastwards from the Oriental-Australasian source area. *Medetera grisescens* is a widespread tramp species, from the western Indian Ocean to Hawaii, while the Australasian *M. salomonis* ranges from French Polynesia to the Philippines. Elements from the predominantly holarctic *apicalis* and *diademaveles* groups are present in the Orient and Australasia. *Medetera kinabaluensis,* from high elevation in Sabah, belongs to the circumboreal, primarily conifer-associated scolytid predator *signaticornis-pinicola* group. The disjunct distribution of the *aberrans* group in the Orient and the New World is regarded as a vicariant distribution resulting from progressive cooling and southward retreat of early Tertiary circumboreal warm mesophytic forests.

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Introduction

Medetera is a cosmopolitan genus of more than 300 described species. The adults are small, mostly dark metallic green flies, often found in numbers on tree trunks where they adopt a characteristic vertical upright posture. In the holarctic region, *Medetera* larvae are often predators of scolytid bark beetle larvae within their galleries, and thus are important biological control agents of these forest pests.

In recent years, major revisions have appeared for the palearctic (Negrobov 1971–77) and the nearctic (Bickel, 1985) *Medetera*. These two faunas constitute a holarctic fauna since a number of species and most species groups occur in both regions. These revisions have provided a morphological and phylogenetic framework for the study of the remaining world fauna.

The present work treats both the Oriental and Australasian *Medetera*. It is useful to consider these two zoogeographical regions together since a number of species occur in both regions, and the Australasian *Medetera*, although with distinctive elements, appears to be derived from the Orient.

Previous workers have described 14 nominal species from the Oriental region (de Meijere, 1916; Becker, 1922; Parent, 1935; Hollis, 1964) and 10 nominal species from the Australasian region, east of Weber's Line (Becker, 1922; Parent, 1932a, 1932b; Parent, 1941; Hardy, 1939; Van Duzee, 1933). This revision recognizes 61 valid species, 43 of them newly described, with 27 Oriental, 29 Australasian and 5 species occurring in both zoogeographical regions. The true diversity of these two regions is probably much larger, since many areas, especially in the Orient, are very poorly collected.

The morphology, bionomics and taxonomy of *Medetera* have been treated extensively by Bickel (1985) and will not be repeated here. Instead, only topics relating directly to Oriental and Australasian *Medetera* or matters needing clarification will be considered in the introductory section.

Materials and Methods

This study is based on specimens of *Medetera* borrowed principally from the Bishop Museum, Honolulu, and supplemented by holdings of Australian, European and North American collections (see Acknowledgements for listings and abbreviations).

Surviving type material of all Oriental and Australasian *Medetera* were examined by me except for *M. adsumpta* Becker and *M. nudicoxa* Becker (both housed at Zoological Survey of India, Calcutta), and *M. longa* Becker (= *M. longicauda* Negrobov & Thuneberg) (surviving syntype, housed at DEI, could not be located; G. Morge, letter). Unfortunately, all dolichopodid types described by Becker (1922) and housed at the Hungarian National Museum, Budapest, are destroyed. In cases where syntypes were placed in other institutions, lectotypes are designated, and neotypes are erected in cases where the original description enabled accurate identification. The types of *M. comes* and *M. palmae*, described by Hardy (1939), could not be located in any Australian collection and are considered lost.

In this study, species are defined primarily on the basis of male genitalia. Isolated females of species lacking diagnostic characters were left unidentified, but usually assigned to a species group. Keys are based on non-genitalic characters where possible, although in most cases accurate identification requires clearing of the male postabdomen.

Drawings of genitalia were made with a camera lucida attached to a compound microscope. The left lateral view is illustrated for all species, supplemented by ventral views of the hypandrium, aedeagus or entire hypopygium. In describing the

hypopygium, 'dorsal' and 'ventral' refer to morphological position prior to genitalic rotation and flexion. Thus, in figures showing a lateral view of the hypopygium, the top of the page is morphologically ventral, while the bottom is dorsal (Fig. 1a).

Features common to a group of species are listed in the introductory discussion and not repeated in species description unless needing clarification. Measurements are in millimetres (mm). The measurements were made on representative specimens (normally the holotype) and should not be considered as invariable for a species. Body length in males is measured from the base of the antennae to the tip of the seventh abdominal segment. Female body length is generally similar to the male of its species unless otherwised noted. Wing length is the perpendicular distance to the apex from an imaginary extension of the humeral crossvein; wing width is measured from the junction of R_1 with the costa to the opposite side of the wing, perpendicular to the wing's long axis (Fig. 1c). The CuAx ratio (termed 'wing ratio' in Bickel, 1985) is the length of the m-cu crossvein/distal section CuA. The position of features on elongate structures is given as a fraction of the total length, starting from the base. The podomere lengths were actual measurements, but should be regarded more as representative ratios. Leg podomere measurements for each leg are given in the formula: trochanter + femur; tibia; tarsomere 1/2/3/4/5. The following abbreviations are used (see Fig. 1b for thoracic chaetotaxy):

I, II, III	pro- , meso-, metathoracic legs
T	tibia
F	femur
ac	acrostichal bristles
a-v	anteroventral
dc	dorsocentral bristles
d-v	dorsoventral
hm	postpronotal bristles
np	notopleural bristles
pa	postalar bristles
pm	presutural supra-alar bristles
ppls	proepisternal bristles
sa	postsutural supra-alar bristles

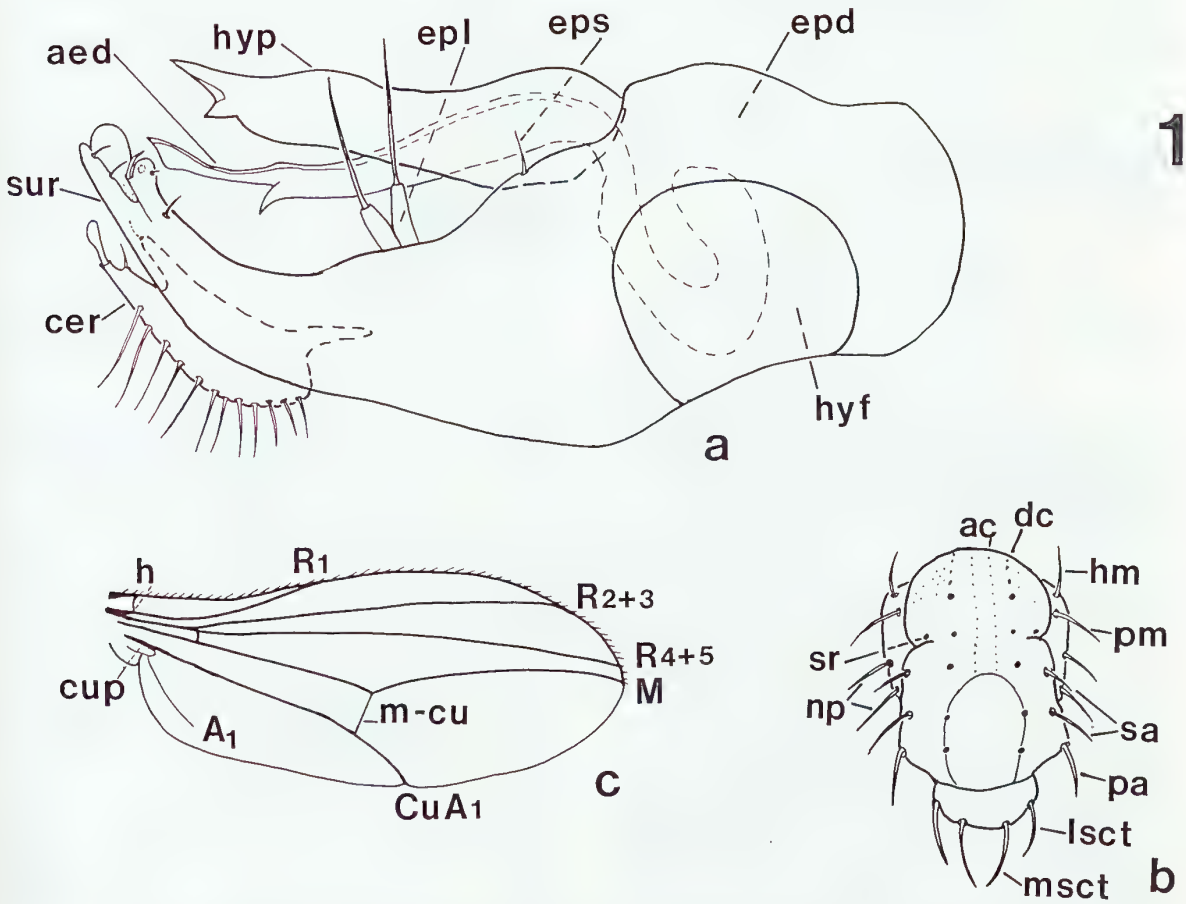

Fig. 1. Morphology of *Medetera* (generalised). **a,** hypopygium, left lateral: aed, aedeagus; cer, cercus; epd, epandrium; epl, epandrial lobe; eps, epandrial seta; hyf, hypopygial foramen; hyp, hypandrium; sur, surstylus. **b,** thoracic chaetotaxy, dorsal view: ac, acrostichals; dc, dorsocentrals; hm, postpronotal; lsct, lateral scutellars; msct, median scutellars; np, notopleurals; pa, postalars; pm, presutural supraalars; sa, postsutural supraalars; sr, presutural intraalars. **c,** wing.

sr	presutural intra-alar bristles
t_{1-5}	tarsomeres 1 to 5
MSSC	Male secondary sexual character(s); nongenitalic characters found only on male body

The Oriental and Australasian zoogeographic regions cover varied landmasses of complex geographical and political association. I have used the term 'Australasian' for the zoogeographical region east of Weber's Line, avoiding confusion between the use of 'Australian Zoogeographical Region' and Australia in the political-geographical sense. Localities are listed under modern political affiliation and follows the "Guide for Contributors to

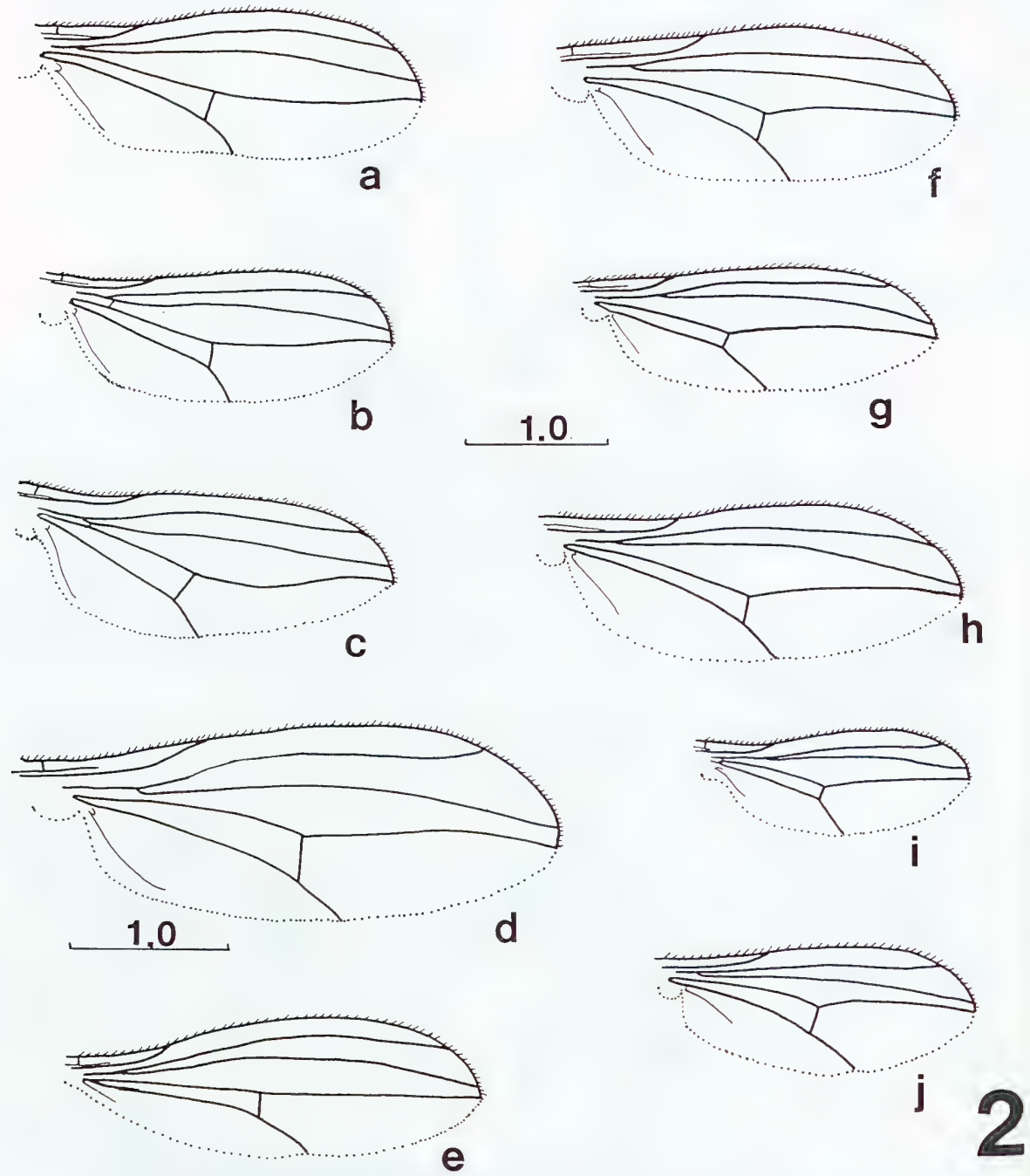

Fig. 2. Right wing, dorsal view: **a,** *M. femoralis;* **b,** *M. salomonis;* **c,** *M. nigrohalterata;* **d,** *M. himalayensis;* **e,** M. gracilis; **f,** *M. austroapicalis;* **g,** *M. flaviscutellum;* **h,** *M. mosmanensis;* **i,** *M. minima;* **j,** *M. platychira.*

the Catalog of Australasian and Oceanian Diptera" (distributed by the Bishop Museum, Honolulu). Thus specimens from the same geographical area might be listed under different headings, for example: Borneo (Indonesia and Malaysia), New Guinea (Indonesia and Papua New Guinea), Samoan Islands (American Samoa and Western Samoa).

Bionomics

Medetera adults characteristically are found in numbers on vertical surfaces such as tree trunks. Here the typical stance of the genus is most evident, the head always facing upwards and the forelegs positioned so that the body is leaning outwards from the surface. If disturbed, they fly directly outwards from the surface and land a short distance away. At other times they run a short way to the side or backwards, without turning, always maintaining the upright position. When flying to a new position on a tree trunk, they generally land diagonally higher, about ¼ to ⅓ the circumference of the trunk with each move. Thus, they tend to spiral up the trunk in progressive steps. On large, smooth-barked eucalypts in Australia, I have observed *Medetera* gradually working their way up a trunk in a spiral fashion until out of sight. *Medetera* often congregate at tree bases and rest there.

The aggregations of *Medetera* on tree trunks serve to facilitate mating and should be regarded as leks, or mating assemblies. Not all trees are equally favored as assembly sites. Smooth-barked trees seem more attractive than trees with rough, gnarled bark. In Australia, for example, smooth barked *Eucalyptus* spp. and *Angophora* spp. are favored in dry and wet sclerophyll forest habitats, while in closed forest, smooth barked palms such as *Archontophoenix cunninghamiana* and other trees are favoured. This is understandable in that individuals would be able to see each other more readily on smooth bark.

In the usual mating sequence, the male approaches the female from behind and arches over the receptive female so that he occupies a position dorsal and posterior to her. He then curls his abdomen forward so that the hypopygium is thrust forward between his legs, with the surstyli and cerci clasping the distal end of the female's abdomen. This sequence of mating behaviour, described in detail by Bickel (1985), has also been observed in Australian *M. grisescens* and *M. nigrohalterata*. The courtship behaviour of those species with obvious male secondary sexual characters, such flattened foretarsi of the *aberrans* group and *M. killertonensis*, or orientated silvery body pruinosity, is unknown.

Although the larval associations of many holarctic *Medetera* species are fairly well known, almost nothing is known of the immature stages of the Oriental and Australasian species. Most *Medetera* larvae are subcortical predators and live under the bark of dead or dying trees. Species have also been reared from bracket fungi and decaying cacti, which are extensions of the subcortical environment. The association of *Medetera* with scolytid bark beetle galleries in the Holarctic is well documented. Not only have female *Medetera* been observed to oviposit at gallery entrances, but they are known to utilize bark beetle aggregation pheromones to locate infested trees. The only known larval host association from the Oriental and Australasian regions is that of *M. nigrohalterata* having been reared from grass tree, *Xanthorrhoea* sp. (Xanthorrhoeaceae) in the Australian Capital Territory.

In Australia, *Medetera* appears to be more abundant and diverse in tropical and subtropical closed and wet sclerophyll forests, and less successful in cooler and drier habitats. This reflects a moist tropical origin for the Australian fauna (see Zoogeography). Only one species, *M. nigrohalterata*, is commonly found in the forests of southern and south-western Australia, and I have seen no Tasmanian specimens. In drier habitats, *Medetera* perhaps faces competition from another medeterine genus, *Corindia* (Bickel, 1986a). The two genera belong to the same ecological guild and they utilize tree trunks in a similar manner. *Corindia* is often abundant in dry sclerophyll forest and occurs across monsoonal northern Australia where *Medetera* is rarely found. *Corindia* possibly is able to outcompete *Medetera* in these more xeric habitats.

Taxonomy

Genus *Medetera* Fischer von Waldheim

Medetera Fischer von Waldheim 1819: 7 (as genus).Type species, *Medetera carnivora* Fischer von Waldheim (monotypy) (=*Musca diadema* Linnaeus).

Oligochaetus Mik, 1878: 7 (as genus). Type species, *Medeterus plumbellus* Meigen, 1824 (orig. designation).

Saccopheronta Becker, 1914: 125 (as genus). Type species, *Saccopheronta nudipes* Becker, 1914 (monotypy).

Elongomedetera Hollis, 1964: 26 (as genus). Type species, *Elongomedetera thoracica* Hollis, 1964 (orig. designation).

Asioligochaetus Negrobov, 1966: 877 (as subgenus). Type species, *Oligochaetus vlasovi* Stackelberg, 1937 (orig. designation).

Lorea Negrobov, 1966: 878 (as subgenus). Type species, *Medetera spiniger* Stackelberg, 1937 (orig. designation).

The name *Medetera* was originally used in the feminine although many authors, including de Meijere (1916), have incorrectly used the masculine form, *Medeterus*.

Medetera is the principal genus of the dolichopodid subfamily Medeterinae, which is superficially distinguished from all other dolichopodid subfamilies by the following combination of characters: mesoscutum distinctly flattened posteriorly; femora II and III lacking anterior preapical bristles; antennal scape without dorsal

setae; arista apical; postcranium strongly concave dorsally; vein M unbranched and lacking a flexion in the distal sector; frontoclypeal suture distinct, usually marked by a band of pruinosity; hypopygium large, on elongate peduncle formed by abdominal segment 7; epandrium distally with surstyli, each divided into dorsal and ventral arms; epandrial seta present ventrobasally; pair of epandrial lobes arising distally along ventral margin near base of surstylus, each lobe bearing strong bristle (for further information on the Medeterinae, see Negrobov, 1971–77 and Bickel, 1985). The five included Australian genera, *Medetera, Atlatlia, Systenus, Corindia* and *Thrypticus* are considered in Bickel, 1986a, 1986b, 1986c, and the present work.

Diagnosis. Eyes bare; proboscis usually heavily sclerotized; 2 sa present, posterior stronger and anterior weaker; coxa III with only 1 lateral seta; femur II without posterior subapical seta; wing veins M and R_{4+5} distinctly bowed anteriorly distad of m-cu crossvein, and converging towards wing apex; anal vein usually distinct.

Medetera is a genus of relatively small dolichopodids, 1.2 to 5.0 mm in length, usually dark metallic green to black, the colouration often obscured by waxy grey or brown pruinosity, but sometimes bright metallic green, little obscured by pruinosity. The genus has a distinctive habitus and life stance which, with little practice, is easily recognized by the unaided eye.

Morphological Notes

1. The secondary segmentation and articulation of the male cercus in the *salomonis* group is unique among Brachycera. Here the cercus has been divided into discrete basal and distal sections, with the distal section freely articulated on basal section and folding back on it, not unlike the blade of a pocket knife (Figs 14c–d; 15a, c, e-f). The distal section is often greatly expanded, sometimes with a corresponding reduction of the surstylus.

2. An unusual combination of a weakly sclerotized and unmelanized postabdomen and basal epandrium occurs in three species of the *melanesiana* group: *M. macalpinei, M. rhetheura* and *M. niuginiensis*. Here the distal half of segment 6, all of segments 7 and 8, and basal portion of epandrium are pale cream and weakly sclerotized, contrasting strongly with the preceding metallic green segments and distal epandrium. This lack of sclerotization and melanization seems to occur in conjunction with a tendency for the hypopygial foramen to become basal in position (see Fig. 6a,f).

3. Prolongation of thorax with increased separation of coxae I and II, prolongation of the legs, and reduction of anal angle (Fig. 2e) are marked tendencies in the *gracilis* group, being best developed in *M. gracilis* itself. These trends show a marked convergence with the habitus of many 'stilt-legged flies' such as Micropezidae. Although nothing is known of the biology of *M. gracilis*, perhaps this species has adopted habits similar to the micropezids, being primarily cursorial and possible ant mimics.

4. Three related high-altitude species from the Himalayas, *M. stomias, M. nepalensis* and *M. himalayensis* have relatively long and broad wings, the wing length being distinctly longer than body length (in most *Medetera* species, the wing is shorter than or at most subequal to the body length). This wing prolongation is possibly an adaptation to high altitude conditions. However, the correlation of increased wing length with increased altitude has not been noted in any other insect group. A far more common trend among high altitude flies is the reduction and loss of wings, leading to flightlessness (Mani, 1968).

5. The proboscis is greatly enlarged and projecting in *M. stomias* (Fig. 17f–g).

6. Most members of the *toxopeusi, flaviscutellum* and *gracilis* species groups have a yellowish scutellum, posterior mesonotum, and postpronotum, contrasting with the generally darker metallic thoracic colouration. The extent of the yellowish colouration appears to vary intraspecifically among specimens. There appears to be no sharp delimitation between yellowish and metallic areas, since it is possible to detect incipient darkening on yellowish cuticle. The more rubbed, possibly older specimens often appear metallic green with only the scutellum and mesonotal depression retaining a yellowish colour, suggesting increasing melanization of the yellowish areas with age.

7. Male Secondary Sexual Characters (MSSC):

a. Flattened foretarsi. In the *aberrans* group, tarsomeres 2–3 on male leg I are usually flattened and modified (Fig. 3b,e). *Medetera killertonensis* has male leg I tarsomeres 3–5 flattened and black, forming an ovate 'flag' (Fig. 12f).

b. Distinctive leg setation is present on males in the *salomonis* group (*M. mooneyensis* and *M. femoralis* with ventral spine-like setae on FII), *flaviscutellum* group (*M. dorrigensis* with ventral dark spine-like setae on FII) and *melanesiana* group (*M. macalpinei* and *M. rhetheura* with FIII setae) (Fig. 6e,h).

c. *Medetera wongabelensis* has patches of anterior silvery hairs on the basal ½ to ⅔ of each tarsomere 1–3 on leg I, giving appearance of 3 silvery patches separated by darker integument.

8. Orientated silvery pruinosity:

a. In the *gracilis* group and on *M. pumila* (*apicalis* group) patches of orientated pruinosity are present on the thorax, legs, abdomen of both sexes (Fig. 11b), appearing grey in lateral view but bright silvery when viewed from between an angle of 0–45 degrees either side of the median sagittal plane.

b. In the *salomonis* group, only male *M. austrofemoralis* have orientated silvery pruinosity on the pleura and legs II and III (MSSC) while in *M.*

femoralis, both male and female have a similar orientated pruinosity.

Some female *Medetera* species show apparently male secondary sexual characters (e.g., orientated silvery pruinosity, noted above, and distinctive leg setation of female *M. dorrigensis).* This might reflect a secondary (and sometimes weaker) expression in females of what was originally only a male character.

Key to Males of Oriental and Australasian *Medetera*
(excluding *M. adsumpta* Becker and *M. nudicoxa* Becker)

1. Tibia longer than femur on all legs; abdominal segment 7, the hypopygial peduncle, twice as long as segment 6 (Fig. 20d); 3 strong dc, decreasing anteriorly (SE Asia) ..... *M. longa*

—— At least FI longer than TI; hypopygial peduncle usually short, not much longer than segment 6; dc various 2

2. Mesonotum bright metallic green or blue-violet, with little pruinosity; distal section of vein M close and subparallel to R_{4+5} (Fig. 2j); FII and/or FIII with strong, usually pale anterior and anteroventral setae; dorsal arm surstylus prolonged, with ventral arm reduced to subtending lobe or lost; male TIII with black apical tooth which is received into excavation on $IIIt_1$ (*aberrans* and *melanesiana* groups) 3

—— Mesonotum dark metallic green or black, or with posterior mesoscutum and scutellum brownish, and usually with dense pruinosity; wing veins various (Fig. 2a–i); FII and FIII with normal vestiture; dorsal and ventral surstylar arms usually subequal; male TIII normal 13

3. Face and clypeus coriaceous blue-green, obscured by pruinoisty; antenna usually with yellowish segments; tarsomeres 2–3 of male leg I often flattened; epandrium cylindrical; hypopygial foramen always left dorsal in position (*aberrans* group) 4

—— Face and clypeus shining blue-violet, with no pruinoisty; antenna black; male leg I normal; epandrium dorsoventrally flattened; hypopygial foramen usually basal in position (*melanesiana* group) 8

4. Cercus with distinct elongate ventrolateral digitiform projection 5

—— Cercus lacking ventrolateral digitiform projection 7

5. Dorsal surstylar arm greatly expanded and rounded apically, clavate (Fig. 4a) (Philippines) ..... *M. luzonensis*

—— Dorsal surstylar arm parallel-sided 6

6. Apex of surstylus with branched modified seta; tarsomeres 2–3 on leg I flattened and ventrally concave (Fig. 3b); ventrolateral cercal projection relatively short (Fig. 3a) (widespread Oriental) ..... *M. platychira*

—— Apex of surstylus with normal setae only; tarsomeres 2–3 on leg I only slightly flattened; ventrolateral cercal projection long and stout (Fig. 3c) (Philippines) ..... *M. mindanensis*

7. Cercus blunt, distally upturned; dorsal surstylar arm reduced to small thumblike projection on ventral arm (Fig. 3d–e); tarsomere 3 only of leg I expanded, with apical curved projection (Fig. 3f); thoracic setae black (New Guinea) ..... *M. gomwa*

—— Cercus boat-shaped, with strong ventral margin and curved subapical setae; surstylus elongate, ribbon-like (Fig. 4b); (leg I missing on specimen); thoracic setae yellow (Borneo) ..... *M. maai*

8. Coxa I and basal ⅔ of femur I dark brown; thorax shining metallic blue violet; thoracic setae black 9

——Coxa I and all femora at least partially yellow; thorax usually metallic green or blue-green; thoracic setae yellowish 10

9. Abdomen entirely dark metallic green; aedeagus lacking internal appendix; pedicels of epandrial lobes weakly developed but present; ventral surstylar arm present as stub; dorsal surstylar arm not capitate (Fig. 5a–b) (New Guinea) ..... *M. morobensis*

——Abdomen often with distal half of segment 6, all of segments 7 and 8, and basal portion of epandrium pale cream colour and weakly sclerotized, contrasting with metallic green of anterior segments; aedeagus with internal appendix; pedicels of epandrial lobes absent; surstylus strongly curved and relatively short, and capitate (Fig. 5d) (New Guinea) ..... *M. niuginiensis*

10. Abdomen with distal half of segment 6, all of segments 7 and 8, and basal portion of epandrium pale cream and weakly sclerotized, contrasting with metallic green of anterior segments; hypopygial foramen basal, only slightly left lateral in position 11

——Abdomen entirely metallic green; hypopygial foramen left dorsolateral 12

11. FIII with long anteroventral setae (Fig. 6e); surstylus relatively short, with capitate arm; epandrium basally truncate (Fig. 6a–d) (New Guinea, Queensland) ..... *M. macalpinei*

——FIII ventrally with long pale ventral seta at ¼, about as long as entire femur (Fig. 6h); surstylus prolonged and narrow, with arms arched medianly; epandrium basally bent, elongate (Fig. 6f–g) (New Guinea) ..... *M. rhetheura*

12. Aedeagus with internal appendix; surstylus curved, with distinctive ventral striated projection and various strong curved apical setae (Fig. 5e). (Melanesia, northern Queensland) ..... *M. melanesiana*

——Aedeagus lacking internal appendix; surstylus short, rounded, capitate (Fig. 5c)(New Guinea) ..... *M. kokodensis*

13. 4–6 strong dc present, decreasing in size anteriorly 14

——Only 2 strong dc present, bordering mesoscutal depression, strongly contrasting with anterior short setulae 31

14. Cercus divided into articulating basal and distal sections, with distal cercus often expanded; vein M bowed posteriorly (Fig. 2a–c); TIII with strong subapical dorsal seta; scape and pedicel usually yellowish (*salomonis* group, part) 15

——Cercus undivided; vein M usually bowed anteriorly (Fig. 2d–i); antenna colour various 18

15. Legs black; aedeagus recurved within epandrium, and with dorsoapical triangular projections; surstylus broad; distal section of cercus curved with apical cuticular projections, and with strong ventrobasal curved seta and midventral blade-like projection (Fig. 14d)(Malaya) ..... *M. malayensis*

——At least tibiae yellowish; aedeagus not recurved within epandrium, and simple distally; other hypopygial features variable 16

16. Pleura and coxa I with dense silvery orientated pruinosity; FI with long black pv setae; FII with row of 7–8 black spine-like ventral setae; wing membrane milky; M almost straight, gradually approaching R_{4+5} (Fig. 2a); surstylus as curved tapering arm; distal cercus greatly expanded with strong ventral seta (Fig. 15e) (New Guinea) ..... *M. femoralis*

——Pleura and coxa I without silvery pruinosity; legs without distinctive setation; wing membrane hyaline; venation and details of hypopygium otherwise 17

17. M and R_{4+5} somewhat bowed (Fig. 2b); epandrial lobes subequal; side lamella present along ventrolateral wall of genital chamber; surstylus curved and broad; distal cercus with ventrobasal triangular structure, midventral lobe, and 2 outer elongate finger-like projections (Fig. 15a–b) (widespread Australasia, Philippines) ..... *M. salomonis*

—— M almost straight, gradually approaching R_{4+5} (as in Fig. 2a); distal epandrial lobe larger than basal lobe, with stout, elongate pedicel and strong bristle, (Fig. 15c–d); surstylus twisted and curved, ribbon-like; distal cercus greatly expanded with large lobate basal portion and narrow outer arm (Melanesia, Queensland) ..... *M. pseudofemoralis*

18. With 5–6 strong dc, decreasing in size anteriorly 19

—— With only 4 strong dc, decreasing in size anteriorly, with the anteriormost strong dc (usually at level of mesoscutal suture) at least 3 times as long as anterior short setulae 20

19. Scape and pedicel yellow; cercus massive, hemispheroidal in dorsal view, without apical blade-like setae; epandrial lobes separate large cylindrical bases, positioned laterad of each other (Fig. 19a–b); lower calypter yellow with dark brown rim (Sabah) ..... *M. kinabaluensis*

—— Antenna black; cercus relatively short, with 2 strong apical blade-like setae; epandrial seta strong, arising from short pedicel (Fig. 14a); lower calypter entirely yellow (south-east Asia to New Guinea) ..... *M. olivacea*

20. Aedeagus in ventral view with subapical anchor-shaped apical hooks; epandrial seta very long, longer than bristles of epandrial lobes; surstylus with 2 very long dorsal setae; cercus short and blunt (Fig. 20a)(Burma) ..... *M. malaisei*

—— Aedeagus tapering; epandrial seta never longer than bristles of epandrial lobes; cercus with apical blade-like setae 21

21. Male basitarsus III with distinct basal anteroventral tooth; hypopygium pyriform, inflated basally; epandrial lobes with bases almost completely fused, forming an elongate collar from which the two bristles arise; hypandrium and aedeagus elongate, narrow, epandrial seta absent (*diadema-veles* group) 22

—— Male basitarsus III without tooth; hypopygium subrectangular; epandrial lobes with bases distinct and separated; hypandrium subrectangular, often basally clasping aedeagus and held out at angle from hypopygium; epandrial seta present (*apicalis* group) 23

22. Lateral scutellars reduced to weak hairs; clypeus dark green to blackish; body length less than 2.0; thorax with 3 brown vittae; dorsoapical blade-like seta tapering with smooth external margin (Fig. 18a)(SE Asia) ..... *M. opaca*

—— Lateral scutellars about ⅔ length of median ones; clypeus satiny metallic blue-green; body length greater than 2.5; thorax with 3 bronze vittae; dorsoapical blade-like seta with weak internal tooth and serrated external margin (Fig. 18b–c) (widespread, common) ..... *M. grisescens*

23. Wing distinctly longer than body (Nepal) 24

—— Wing shorter than or at most subequal to body length 26

24. Proboscis greatly enlarged, almost as long as eye height, and sometimes drawn up flap-like (Fig. 17f–g); cercus stout and curved, without apical blade-like seta; face dark brown with blue reflections; wing membrane hyaline (Fig. 17e) ... *M. stomias*

—— Proboscis normal, much shorter than eye height; cercus with dorsoapical blade-like seta; face metallic blue-violet; wing membrane milky, with contrasting dark brown veins 25

25 Epandrial seta on mound; epandrial lobes with distinct collar-like bases; short setulae present along ventral margin of epandrium between epandrial seta and

epandrial lobes; ventral surstylar arm with simple curved seta; cercus with short blade-like seta and long digitiform projection (Fig. 17c–d). ..... *M. himalayensis*

—— Epandrial seta on flat epandrial margin; epandrial lobes arise from epandrial margin without collar-like bases; ventral epandrial margin bare; ventral surstylar arm with flattened frayed seta; cercus with elongate curved apical seta and ventral costate blade-like seta (Figs 17a-b) ..... *M. nepalensis*

26. Tarsomere 2 distinctly longer than adjacent tarsomere 1 on all legs (Fig. 16b) (Indonesia) ..... *M. longitarsis*

—— At least on legs I and II, tarsomere 1 greater than or subequal to tarsomere 2 on all legs 27

27. Thoracic setae yellow; size small, length < 2.0; face polished green-violet; coxae I and II with bright silvery pruinosity; distal ¼ of hypandrium weakly sclerotized (Fig.17h) (Oriental) ..... *M. pumila*

—— Thoracic setae black; length > 2.0; face with grey pruinosity; coxae without silvery pruinosity; hypandrium equally sclerotized along entire length 28

28. Surstylus expanded dorsally, with cuticular striae; cercus with strong, curved blade-like dorsoapical seta, subtended ventrally by 2 blade-like setae, curled pedunculate seta, and longer straight pedunculate seta; scape and pedicel yellow; epandrial seta strong and midway between epandrial lobe and base of hypandrium (Fig. 16d)(Sri Lanka) ..... *M. chandleri*

—— Surstylus more or less parallel-sided; cercus without curled pedunculate seta, and longer straight pedunculate seta; scape and pedicel various; epandrial seta various 29

29. Scape and pedicel usually yellow, although sometimes strongly infuscated; cercus with thin, curved dorsoapical seta on short cuticular peduncle; cercus with lateral leaf-shaped seta (Fig. 16e)(widespread) ..... *M. austroapicalis*

—— Scape and pedicel always dark brown; cercus with flattened, curved blade like dorsoapical seta 30

30. Segment 7 (hypopygial peduncle) relatively long, about equal to length of epandrium; epandrial seta near base of hypandrium; cercus with apical bladelike seta subtended by subrectangular cuticular projection bearing short apical seta (Fig. 16a)(Philippines) ..... *M. liwo*

—— Segment 7 not much longer than segment 6 or about half length of epandrium; epandrial seta near surstylar lobes; cercus with apical blade-like seta subtended by 2 short rounded setae as in Fig. 16b; (Fig. 16c)(Indonesia) ..... *M. apicipes*

31. Cercus divided into articulating basal and distal sections; vein M bowed posteriorly (Fig. 2a–c); antenna black; TIII with strong subapical dorsal seta; coxae, femora and tibiae dark brown to black (*salomonis* group, part, Australia) 32

—— Cercus undivided; vein M usually bowed anteriorly (Fig. 2d–i); antenna and leg colour various 34

32. Haltere distinctly dark brown to black; lower calypter yellow with brown rim; M slightly flexed just before apex (Fig. 2c); hypandrium with subapical ventral denticles; surstylus curved and with strong ventral seta; distal cercus with ventral rectangular projection basally, clavate distal arm, and expanded midsection (Fig. 14c) ..... *M. nigrohalterata*

—— Haltere and lower calypter entirely yellow; hypandrium with ventral surface bare; surstylus and cercus otherwise 33

33. FII with row of black spine-like setae along entire ventral margin; legs and pleura with grey pruinosity; distalmost epandrial lobe twice as long as proximal lobe but of similar strength; surstylus with ventral costate seta; distal cercus cap-like, with strong, striated, curved dorsoapical seta (Fig. 14b) ..... *M. mooneyensis*

—— FII without spines; pleura, anterior femora and tibiae I and II covered with dense silvery orientated pruinosity; distal epandrial lobe much longer and wider than proximal lobe; surstylus U-shaped; distal cercus elongate, curved, and divided into 3 elongate overlapping sections (Fig. 15f) (Queensland). *M. austrofemoralis*

34. Wing with reduced anal angle (Fig. 2e); ac reduced to absent; face shining metallic blue-violet; lateral scutellars reduced to weak hairs; coxae I, legs mostly yellow; silvery pruinose patches often present on bodies(Fig. 11b) (south-east Asia) (*gracilis* group) 35

—— Wing with distinct anal angle; ac present, short; face usually with pruinosity; lateral scutellars and leg colour various; bodies without silvery pruinose patches 38

35. Scape and pedicel yellow; It_2 shorter than It_1; central surstylar arm distally curved; ventral surstylar arm with digitiform seta; cercus with distinctive ventral pedunculate expanded seta (Fig. 11d) ..... *M. borneensis*

—— Antenna entirely brown; $It_2 > It_1$; surstylus otherwise; cercus lacking with distinctive ventral expanded seta; silvery pruinose patches present on thorax, coxae and abdomen 36

36. Thorax elongate, length more than twice width; length $t_2 > t_1$ on all legs; anal angle highly reduced; distal epandrial lobe with pedicel twice as long as that of basal lobe; surstylus clavate, dorsal surstylar arm with distinctive, stout branched seta (Fig. 11e) ..... *M. gracilis*

—— Thoracic length not more than 1½ width; length $t_2 > t_1$ on I and III only; anal angle not so strongly reduced; surstylus only slightly expanded distally 37

37. Distal epandrial lobe pedicel much longer than that of basal lobe; cercus with 2 distinctive ventral setae: stout triangular apical seta and narrower tapering blade-like seta at ⅔ (Fig. 11a) ..... *M. sandakanensis*

—— Pedicels of epandrial lobes subequal in length; cercus rather stout, with 2 distinctive ventral setae: blade-like apical seta and hatchet-shaped seta at ⅔ (Fig. 11c) ..... *M. penangensis*

38. Aedeagus strongly recurved within epandrium, often reaching base of epandrium before curving back (Figs 8–10) (*australiana* + *toxopeusi* groups) 39

—— Aedeagus not recurved within epandrium, but bent at right angle after entering epandrium 49

39. Cercus with distinctive pilose capitate ventral knob; lower calypter yellow with dark brown rim; length 1.6 or less; antenna black (Fig. 10a–b) (south east Asia) .. *M. vivida*

—— Cercus without pilose capitate ventral knob, but with various projections; lower calypter usually entirely yellow; length usually > 2.0; antenna various 40

40. Antenna entirely black; lateral scutellars about ¾ length of medians; arista about as long as head height; bristle of distal epandrial lobe simple or forked; cercus without apical setal projections and without ventral projections (*australiana* group) (Australia) 41

—— Scape and pedicel yellow; lateral scutellars less than ½ length of medians; arista usually longer than twice head height; bristle of distal epandrial lobe often with numerous hair-like branches; cercus usually with apical modified setal projections and often with ventral lobate projection (*toxopeusi* group) 44

41. Lower calypter entirely pale; coxae and basal ⅔ of femora with bright silvery pruinosity; distance between epandrial lobes much less than distance between basal epandrial lobe and epandrial seta 42

—— Lower calypter pale with distinct brown rim; coxae and femora with grey pruinosity; distance between epandrial lobes greater than distance between basal epandrial lobe and epandrial seta 43

42. Male tarsus I with distinct silvery hairs on basal ½ to ⅔ of It_1, It_2 and It_3; cercus tapering; bristle of distal epandrial lobe forked; dorsal surstylar arm with subapical branched seta (Fig. 8b) ..... *M. wongabelensis*

—— Male tarsus I with pale hairs only; cercus blunt; bristle of distal epandrial lobe simple; surstylar setae as figured (Fig. 8d) ..... *M. queenslandensis*

43. Tibiae yellowish; cercus elongate, tapering; ventral surstylus with striated seta; dorsal surstylar arm elongate with ventral subapical setae as figured (Fig. 8a) ..... *M. mosmanensis*

—— Tibiae dark brown to black; cercus stouter, apically curved; surstylus relatively short, with dorsal arm clavate (Fig. 8c) ..... *M. australiana*

44. Thorax dark metallic green; coxae, basal femora brown 45

—— Thorax metallic green with scutellum, posterior mesoscutum and humeral area yellow-brown; coxa I and all femora yellow 46

45. Surstylus not deeply cleft; cercus with short apical setae; bristle of distal epandrial lobe branched; dorsal surstylar arm curved and capitate (Fig. 9e) (New Guinea) ..... *M. irianensis*

—— Surstylus deeply cleft; cercus blunt apically with medioapical curved bladelike seta and with weak ventral mound which bears 4 setae; bristle of distal epandrial lobe unbranched (Fig. 10c–e) (New Guinea) ..... *M. gressitti*

46. Cercus with long thin apical seta; cercus without distinct ventral projection (Fig. 9d) (New Guinea) ..... *M. papuensis*

—— Cercus with apical blade-like seta; cercus with distinct midventral setose projection 47

47. Distal cercus not greatly expanded, but with large blade-like seta; dorsal surstylar arm with apical spatulate seta (Fig. 9a) (New Guinea, Solomons) ..... *M. cheesmanae*

—— Distal cercus greatly expanded, with setae as figured (Fig. 9b); dorsal surstylar arm without apical spatulate seta 48

48. Ventral surstylar arm with deep V-shaped cleft; dorsal surstylar arm subequal to ventral arm, and with apical setae (Fig. 9c) (New Guinea) ..... *M. toxopeusi*

—— Ventral surstylar arm not so deeply cleft; dorsal surstylar arm longer than ventral arm, and with strong dorsal seta (Fig. 9b) (New Guinea) ..... *M. waris*

49. Small, length 1.8 or less; antenna black 50

—— Larger, length ‘ 2.5; scape and pedicel yellowish 52

50. Cercus without distinct ventral projection, but blunt, with 3 distinct apical blade-like setae; (Fig. 20e) (south-east Asia to Solomons, Queensland) ..... *M. minima*

—— Cercus with distinct ventral knob or projection 51

51. Posterior half of mesonotum brownish; basal half of femora brown; pedicel of distal epandrial lobe twice as long as that of basal lobe; cercus with thin, curved apical seta, and with tapering ventral projection which bears strong apical seta and 3 weaker proximal setae (south-east Asia) (Fig. 7b) ..... *M. bishopae*

—— Mesonotum dark metallic blue-black; femora entirely yellow; distal and proximal epandrial lobes subequal; cercus with curved blade-like apical seta, and with capitate ventral projection which bears 4 subequal setae (Fig. 7a) (Nepal) ..... *M. chillcotti*

52. Scutellum and posterior mesoscutum green, without evidence of yellow colouration 53

—— Scutellum and posterior mesoscutum at least partially yellow-brown in colour 54

53. Ventral surstylar arm striated with subapical setal flag and very long seta projecting from adjacent arm; cercus thin basally, with midventral lobe and thin dorsoapical seta (Fig. 13f) (eastern Australia) ..... *M. gingra*

——Dorsal surstylar arm with distinctive strong cuticular hook; cercus with 2 strong ventral projections as figured (Fig. 13g) (Queensland) ..... *M. bunyensis*

54. Surstylus divided into 3 arms, with distinctive basoventral triangular arm; zone of weakness evident at join between surstylus and epandrium 55

——Surstylus without basoventral triangular arm; surstylus usually solidly fused to epandrium 56

55. Male tarsomeres 3–5 on leg I flattened, black, ovate (Fig. 12f); coxa I brown; lower calypter entirely pale yellow; lateral scutellars reduced to weak hairs; epandrial seta very short, not close to epandrial lobes; dorsal surstylar arm with single apical seta (Fig. 12d–e) (New Guinea) ..... *M. killertonensis*

——Male tarsus I not flattened; coxa I yellow; lower calypter pale yellow with dark brown rim; lateral scutellars about ½ length of medians; epandrial seta very short, close to epandrial lobes; dorsal surstylar arm with strong median cuticular hook and with apical seta (Fig. 12c) (New Guinea) ..... *M. flaviscutellum*

56. Hypandrium with pair of lateral projections arising basally (Fig. 12b); cercus with distinctive set of apical setae including elongate outer seta and leaf shaped inner seta (Fig. 12a) (Queensland) ..... *M. athertonensis*

——Hypandrium without lateral projections (e.g. Fig. 13b); cercus various 57

57. Epandrial lobes strongly diverging and bearing bristles of similar length; dorsal surstylar arm curved, ribbon-like, with strong lateral side seta (Fig. 12g) (Philippines) ..... *M. philippinensis*

——Epandrial lobes subparallel and with bristle of proximal lobe longer than that of distal lobe; dorsal surstylar arm massive, distinctly bent 58

58. FII with 6–7 dark, spine-like ventral setae distally (Fig. 13c); FIII with long pale a-v setae along entire length; ventral surstylar arm with blade-like seta on subtriangular mound; outer strong cercal seta not pedunculate (Fig. 13a–b) (New South Wales) ..... *M. dorrigensis*

——FII with only weak pale hairs ventrally; FIII with only short setae; dorsal surstylar arm strongly developed dorsoapically, and with stout projecting seta; outer strong cercal seta on peduncle (Fig. 13e) (eastern Australia) ..... *M. uda*

The *aberrans* and *melanesiana* Groups

The *aberrans* and *melanesiana* groups share the following features: body colouration bright metallic blue-green to blue-violet, with only thin dusting of pruinosity; dorsal postcranium strongly concave; proboscis relatively small; Ac well developed; Dc strong, prominent, usually 4–5 present; two strong sa present; lateral scutellars well developed, about ¾ length of medians; FIII and sometimes FII in both sexes with 2–5 strong anterior setae; TIII with black, apical tooth-like projection which is received into excavation on $IIIt_1$ (on only Oriental and Australasian *aberrans* group and all *melanesiana* group) (MSSC); wing venation distinctive: M not strongly arched, but lies almost subparallel to R_{4+5} (similar to Fig. 2j); hypandrium arising from approximately halfway along ventral margin; epandrial lobes separate and positioned distad on epandrium, with marked tendency to lose collar-like pedicels, such that the bristles appear to rise directly from ventral margin of epandrium; epandrial seta closer to epandrial lobes than to base of hypandrium; dorsal surstylar arm extending well beyond ventral surstylar arm and often apically expanded; ventral surstylar arm often reduced to seta-bearing mound (apomorphy); cercus with elongate ventrolateral arm, separated by a deep furrow from the more dorsobasal portion (apomorphy).

The *aberrans* and *melanesiana* groups are closely related and the *melanesiana* group appears to have been derived from the *aberrans* group.

The *aberrans* group is characterized by the following features: antenna often yellowish; face and clypeus often with pruinosity; male leg I usually with t_{2+3} flattened and modified (MSSC) (apomorphy);

male TIII with group of pale dorsal subapical setae (MSSC); male postabdomen always strongly melanized and sclerotized; epandrium cylindrical, not strongly flattened; cerci free, not medially fused; hypopygial foramen always left dorsolateral in position.

The *aberrans* group is found in the Nearctic, Neotropical, Oriental and Australasian zoogeographic regions but is particularly diverse in the New World tropics (Bickel, 1985). The five species considered below represent a disjunct or vicariant distribution from the major New World radiation (Fig. 22). There is little doubt that the *aberrans* group is monophyletic, since the hypopygial form, general habitus and colouration, and flattened male foretarsomeres are distinctive for the group. The Oriental *Medetera platychira,* considered below, is strikingly similar to the eastern nearctic *M. aberrans* (see figures in Bickel, 1985). For further discussion, see Zoogeography.

Of the five species considered below, *Medetera platychira, M. maai, M. luzonensis* and *M. mindanensis* are found in the Oriental tropics, while *M. gomwa* is from New Guinea. Most of the specimens were collected from rainforest habitats.

The *melanesiana* group is characterized by the following features: antenna black; face and clypeus usually shiny metallic blue-violet; male leg I normal, without flattened tarsomeres; male femur III with rows of long anterior and anteroventral setae; tendency in some species for the distal half of abdominal segment 6, all of segments 7 and 8, and basal portion of epandrium to be pale cream and weakly sclerotized, in contrast with metallic green of anterior segments (MSSC); tendency for hypopygial foramen to become dorsobasal in position (apomorphy); epandrium strongly flattened dorsoventrally (apomorphy); only single (dorsal) surstylar arm present, and tending towards prolongation (apomorphy) (ventral surstylar arm totally absent or present only as seta-bearing mound); surstylus fused to epandrium, without evidence of suture; aedeagus sometimes with internal appendix; cerci fused medially (apomorphy).

The *melanesiana* group is confined entirely to the Australasian region, from New Guinea to the Solomons and Queensland, and includes 6 species: *M. morobensis, M. niuginiensis, M. macalpinei, M. rhetheura, M. melanesiana* and *M. kokodensis.* The tendency for prolongation of the surstylus and for abdominal segments 6, 7 and 8, and basal portion of epandrium to become pale cream and weakly sclerotized is most marked in *M. rhetheura.*

The *abrerrans* Group

Medetera platychira de Meijere

Medeterus platychirus de Meijere, 1916: 261.

Type material. *Medetera platychira* was described from a syntype series of 6♂♂ and 3♀♀ taken in Java. I have designated a male, bearing the label "Batavia/ i-1907/ Jacobson", as lectotype (ZMUA, examined). A female from Malaya bearing a Parent holotype label with the name "*Medetera luteinervis*" (BMNH) represents an unpublished manuscript name and is identical in all respects with females of *M. platychira.*

Additional material. Hong Kong: Taipohau, Kowloon, Sheng Shui District, 15 June to 24 Sept 1965 (BPBM). **Indonesia:** Sumatra, Anai Kloof, 500 m, 1926 (BMNH). **Malaysia:** Sarawak: Sandong, Kampong, Tapuh, 300–400 m, 4–9 July 1958; Nanga Pelagus, near Kapit, 180–585 m, 7–14 Aug 1958; Pueh Lundu District, Kampong, 690–1500 m, 6–12 June 1958. Sabah: Ranau, 500 m, 28 Sept to 7 Oct 1958; Liawa, 15 Jan 1959; Tawa Residency, Kalabakan River, Tawau, 9–18 Nov 1958 (all BPBM). West Malaysia: Cameron Highlands, Mt Brichang, 5 Jan 1959 (BPBM); Perak Batang Padang, 360 m, 8 March 1925; Selangor Bukit Kutu, 10 Jan 1973 (BMNH). **Nepal:** (♀♀ only) Lothar, near Birganj, 135 m, 11 Sept 1967 (CNC). **Philippines:** Luzon, Mt Montalban, 150–200 m, 14 March 1965; Mindanao, Agusam, S. Francisco, 14 Nov 1959; Misamis Or, Balason, 4–5 April 1960 (all BPBM). **Sri Lanka:** Kandy District, Perideniya Mahawali River, 23 Feb 1974 (BMNH); Kohuwala W.P., 31 Nov 1966 (CNC). **Taiwan:** Taihorin, July 1917 (ZMH). **Thailand:** Chiangmai Province, Doi Suthep, 3 April 1958 (BPBM). 38♂♂, 28♀♀ specimens examined. In addition, Becker (1922) recorded this species from Bangladesh and West Bengal, India.

Description. Male: length 2.5–2.8; wing dimensions 2.7 x 1.0.

HEAD: vertex, frons, face, clypeus dark metallic bluegreen, with some grey pruinosity; proboscis dark brown; scape and pedicel dark brown; 1st flagellomere yellowish; arista about as long as head height.

THORAX: dorsum metallic green with dusting of silvery pruinosity; pleura covered with dense silvery pruinosity; setae black, and strongly developed; 10–12 pairs ac, increasing in length posteriorly, length of posteriormost 1½ times longer than width of ac band; 4 strong dc present, decreasing anteriorly, with 7–8 short setulae anteriormost.

LEGS: coxae, trochanters and basal ⅔ of femora dark brown, remainder of legs yellow; relative podomere ratios as I: 1.5; 1.4; 0.7/0.4/0.3/0.2/0.2; It_{2-3} flattened and ventrally concave (Fig. 3b) (MSSC); II: 1.9; 1.4; 0.9/0.4/0.3/0.2/0.2; TII with strong subapical ventral seta; III: 2.4; 2.5; 0.6/0.9/0.7/0.4/0.2.

WING: M not strongly arched, but almost subparallel with R_{4+5} (Fig. 2j); CuAx ratio 0.6; lower calypter yellow with fan of yellowish setae; haltere yellow.

ABDOMEN: bright metallic green with dusting of grey pruinosity and with short pale setulae; segment 7 not greatly elongated; hypopygium dark brown with yellowish cerci (Fig. 3a); epandrium elongate, oblong, with hypandrium arising from beyond midventral position; hypandrium simple, relatively short; aedeagus simple, with sharp dorsoapical projections; epandrial seta weak, positioned near epandrial lobes;

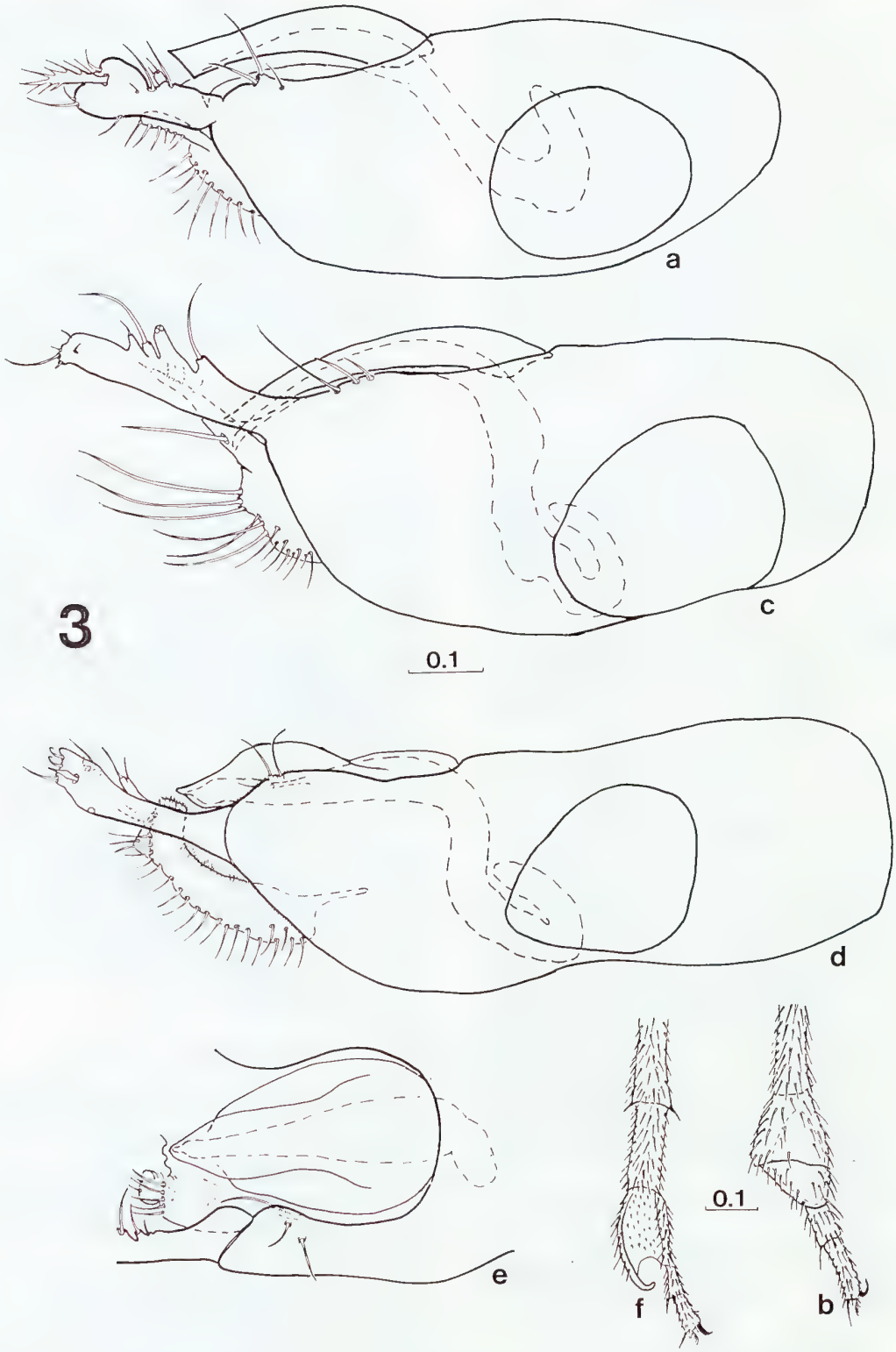

Fig. 3. a–b, *M. platychira,* Java; a, hypopygium, left lateral view; b, male left tarsus I, dorsoposterior view. **c,** *M. mindanensis,* Mindanao; hypopygium, left lateral view. **d–f,** *M. gomwa,* Fergusson Island, Papua New Guinea; d, hypopygium, left lateral view; e, left hypopygium, dorsal view; f, male left tarsus I, dorsal view.

basal epandrial lobe with distinct collar-like pedicel, but distal lobe with bristle only, lacking pedicel; surstylus relatively short, fused to epandrium, join marked by dorsal and ventral indentations; ventral surstylar arm as short projection arising from dorsal arm; dorsal surstylar arm somewhat expanded distally, bearing distinctive branched seta and other setae as figured; cercus rounded basally and separated by furrow from distal arm-like projection.

Female: similar to male except lacking MSSC.

Remarks. *Medetera platychira* is widely distributed across the Oriental region, in an area bounded by Sri Lanka, lowland Nepal, southern China, the Philippines and eastern Indonesia (Fig. 22). The branched surstylar seta varies somewhat among specimens. This species bears a close resemblance to the nearctic *M. aberrans.*

Medetera mindanensis n. sp.

Type material. HOLOTYPE ♂: **Philippines:** Mindanao, Lanao, Butig Mtns, 24 km north-east of Butig, 1080 m, light trap in rainforest, 20 June 1958, H. E. Milliron (BPBM).

Other material. Possible ♀: **Philippines:** Camarine Sur, Mt Isarog, 20 km east of Naga, 500–600 m, 7 April 1963 (BPBM).

Description. Male: length 2.7; wing dimensions, width 2.6 x 1.0; similar to *M. platychira* except as noted.

THORAX: dorsum metallic green with brownish pruinosity.

LEGS: colouration, relative podomere ratios and setation similar except as noted: It_2 only slightly expanded apically; It_3 distinctly widened and flattened, at least twice as wide as It_4 (MSSC).

WING: CuAx ratio 0.7; lower calypter yellow with fan of black setae.

ABDOMEN: dark metallic green with short black setulae; hypopygium dark brown with yellowish cerci (Fig. 3c); epandrium oblong, subrectangular; hypandrium and aedeagus simple; epandrial seta positioned distad, near epandrial lobes; epandrial lobes represented by bristles only, collar-like bases not evident, and distal bristle longer than basal bristle; surstylus with 4 ventral cuticular projections which bear setae as figured, and second basal projection probably represents remnant ventral surstylar arm; cercus tapering, bearing strong dorsal setae on basal half and distally with 4 short ventral setae and short apical seta.

Female: similar to male except without modified It_{2-3}.

Remarks. *Medetera mindanensis* is restricted to the Philippine Islands and appears to be closely related to *M. luzonensis.*

Medetera gomwa n. sp.

Type material. HOLOTYPE ♂, PARATYPE ♂: **Papua New Guinea:** Fergusson Island, Deidei, Gomwa Bay, 0–20 m, 2–6 July 1956, Fifth Archbold Expedition to New Guinea, L. J. Brass (AMNH).

Description. Male: length 2.4; wing dimensions 2.0 x 0.8; similar to *M. platychira* except as noted.

HEAD: scape and pedicel brown, 1st flagellomere missing.

THORAX: 2 strong dc bordering mesoscutal depression, with somewhat shorter anterior dc near mesonotal suture, and 7–8 short setulae anteriormost.

LEGS: coxae and femora dark brown to femoral 'knees'; remainder of legs yellow, although distal tarsomeres darkened; relative podomere ratios similar; It_3 expanded with apical projection (Fig. 3f) (MSSC).

WING: similar to Fig. 2j, but M and R_{4+5} not as close to each other; CuAx ratio 0.8.

ABDOMEN: bright metallic green with dusting of grey pruinosity; hypopygium dark brown with yellowish cerci (Fig. 3d); epandrium elongate, with hypandrium arising at ⅔ along ventral margin; hypandrium in lateral view appearing ventrally sinuate; hypandrium in ventral view (Fig. 3e) with sinuate region appearing to arise from broad base; aedeagus simple; epandrial seta arising from elongate collar-like pedicel lying hidden from external view along lateral margin of genital chamber; epandrial lobes lacking collar-like bases and only represented by two relatively short bristles; surstylus with short ventral arm arising from elongate dorsal arm; dorsal surstylar arm with blade-like seta and other setae as figured; cercus with upturned blunt apex and with dorsal setae as figured.

Female: unknown.

Remarks. *Medetera gomwa* occurs in New Guinea and is the only member of the *aberrans* group east of Weber's Line. The cercus is unique in having a blunt upturned apex, and in lacking the basal furrow and ventrolateral arm. Only It_3 is flattened in the male, whereas in *M. platychira* and *M. mindanensis,* both It_3 and It_2 are flattened.

Medetera luzonensis n. sp.

Type Material. HOLOTYPE ♂: **Philippines:** Luzon, Rizal Province, Wa-Wa Dam, Mt Montalban, 150 m, light trap, 13 March 1965, H. M. Torrevillas (BPBM).

Description. Male: length 2.0; wing dimensions 1.8 x 0.7; holotype somewhat rubbed, missing thoracic setae and distal leg I; similar to *Medetera platychira* except as noted.

HEAD: antenna entirely yellow.

THORAX: dorsum bright metallic green with dusting of grey pruinosity; setae yellowish.

LEGS: coxae and basal half of femora brown, remainder of legs yellow; relative podomere ratios as: I: 1.8; 1.5; remainder of leg I missing; II: 2.0; 1.7; 1.1/0.4/0.3/0.2/0.2; TII with strong pale ventral

subapical seta; III: 2.0; 2.4; 0.5/0.9/0.6/0.3/0.2.

WING: CuAx ratio 0.6.

ABDOMEN: bright metallic green with short pale setulae; hypopygium dark brown with yellowish cerci (Fig. 4a); epandrium elongate, with hypandrium arising at ⅔ along ventral margin; hypandrium and aedeagus simple; epandrial seta positioned distad, near epandrial lobes; epandrial lobes represented by bristles only, collar-like pedicels absent; surstylus elongate, with 4 ventral cuticular projections, each bearing apical seta; surstylus with weakly sclerotized, apically expanded clavate projection; cercus basally expanded, separated by furrow from ventrodistal projection which bears setae as figured; apical portion of cercus possibly missing.

Female: unknown.

Remarks. Since leg I of the male specimen is missing, it is not known if It_{2+3} are expanded.

Medetera maai n. sp.

Type material. HOLOTYPE ♂: **Malaysia:** Sarawak, Bau District, Pangkalan Tebang, 300–450 m, Sept 1958, T. C. Maa (BPBM).

Description. Male: length 2.0; wing dimensions 2.0 x 0.8; specimen somewhat rubbed.

HEAD: vertex, frons metallic green with grey pruinosity; face, clypeus shining metallic blue with dusting of pruinosity; proboscis brown; scape and pedicel black, 1st flagellomere missing.

THORAX: dorsum metallic blue-green; setae missing but pale coloured.

LEGS: coxae, femora brown to femoral 'knees', remainder of legs yellow; relative podomere ratios as: I: missing; II: 2.5; 2.3; 1.2/0.6/0.4/0.3/0.2; TII with strong apical ventral seta; III: 2.8; 3.0; 0.7/1.3/0.7/0.5/ remainder missing.

WING: similar to Fig. 2j; CuAx ratio 0.7; lower calypter yellow with fan of pale setae; haltere yellow.

ABDOMEN: metallic green-bronze with short pale setulae; hypopygium dark brown with yellowish cerci (Fig. 4b); epandrium elongate, with hypandrium arising at approximately midventral position; hypandrium and aedeagus simple; epandrial seta absent; epandrial lobes with short collar-like bases, and positioned near base of surstylus; surstylus fused to epandrium and elongate, ribbon-like, with setae as figured; surstylus with 2 arms, corresponding to dorsal and ventral surstylar arms, and ventral surstylar arm longer; cercus boat-shaped, with strong ventral margin or costa, distally bearing strong dorsally projecting curved setae, and basally with strong dorsal seta.

Female: unknown.

Remarks. *Medetera maai* has a rather unusual ribbonlike surstylus and a distinctive boat-shaped cercus. Although leg I is missing, I have associated this species with the *aberrans* group based on similarity of MSSC and general habitus.

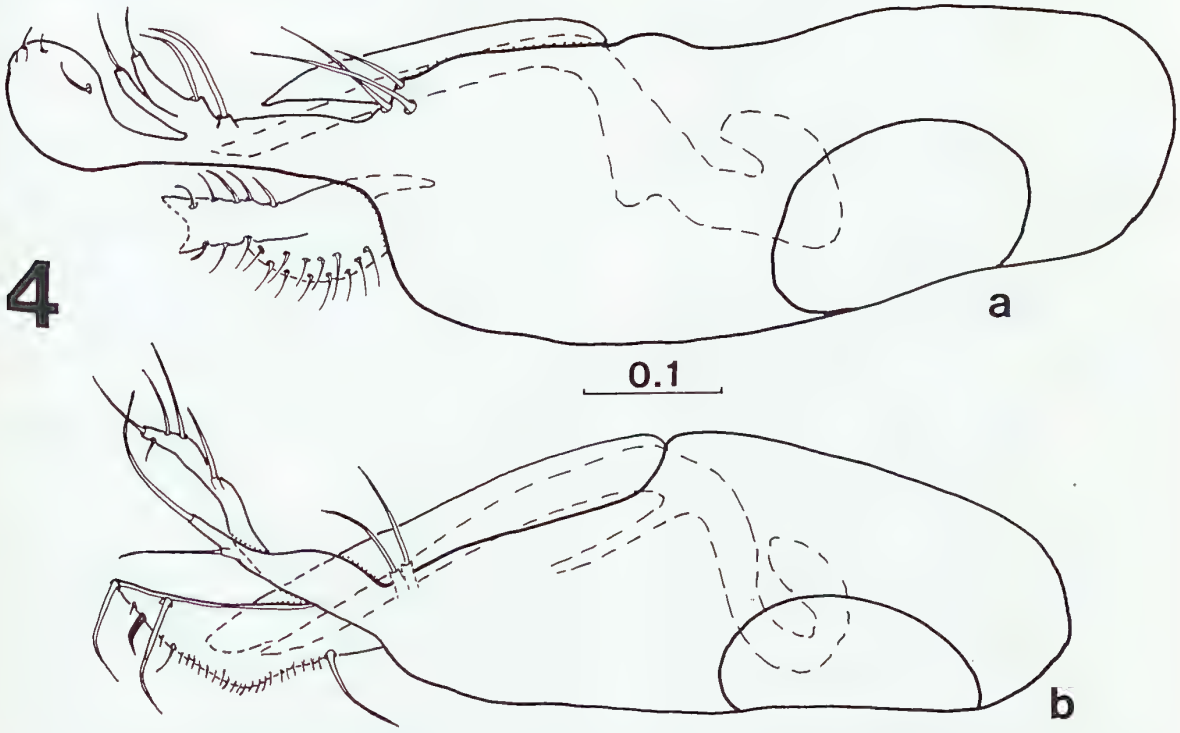

Fig. 4. a, *M. luzonensis,* Luzon; hypopygium, left lateral view. **b,** *M. maai,* Sarawak; hypopygium, left lateral view.

The *melanesiana* Group

Medetera melanesiana n. sp.

Type material. HOLOTYPE ♂: **Solomon Islands:** Vella Lavella, Ulo Crater, 10 m, malaise trap, 21 Dec 1963, P. Shanahan (BPBM). PARATYPES: **Australia:** 1♂, 1♀, Queensland, Iron Range, 16 Aug 1971 (ANIC); **Indonesia:** Irian Jaya: 2♂♂, Nabire, 5–50 m, 25 Aug to 2 Sept 1962; 1♂, Waris, south of Jayapura, 450–500 m, 8–15 Aug 1959 (BPBM); **Papua New Guinea:** 2♂♂, Central Province, Laloki, 15 May 1984, (PDPI); ♂, New Britain, Gazelle Peninsula, 130 m, 28 Oct 1962 (BPBM).

Additional material. Probable ♀♀: **Papua New Guinea:** Maprik, 160 m, 29 Dec 1959 to 17 Jan 1960 (BPBM). **Solomon Islands:** Santa Ysabel, south of Tatumba, 0–50 m, 8 Nov 1964 (BPBM).

Description. Male: length 2.0; wing dimensions 1.9 x 0.7.

HEAD: vertex and frons metallic blue-green, covered with dusting of grey pruinosity; face and clypeus shining metallic blue-violet; proboscis dark brown, not strongly developed; arista with short hairs, and about as long as head height.

THORAX: dorsum bright metallic blue-green with dusting of grey pruinosity; pleura covered with dense grey pruinosity; setae yellow; 6–7 pairs ac, well developed and longer than width of ac band; 4 strong dc, decreasing anteriorly with short setulae anteriormost; lateral scutellars ¾ length of medians.

LEGS: coxae brownish basally and anteriorly on I and II; distal coxae and remainder of legs yellow; leg setae yellow; relative podomere ratios as I: 2.1; 1.8; 0.7/0.6/0.4/0.3/0.2; II: 2.2; 2.1; 1.1/0.6/0.5/0.3/0.2; TII with strong subapical ventral seta; III: 2.4; 2.5; 0.6/1.0/0.5/0.3/0.2; FIII with anterior and anteroventral rows of long pale setae (MSSC).

WING: M not strongly arched, but lies almost subparallel with R_{4+5}, similar to Fig. 2j; CuAx ratio 0.6; lower calypter yellow with fan of yellowish setae; haltere yellow.

ABDOMEN: entirely dark metallic green with bronze reflections, with dusting of grey pruinosity, and with short pale setulae; hypopygium dark brown with yellowish cerci (Fig. 5e); epandrium strongly flattened, subrectangular, elongate, with hypandrium arising from midventral position; hypopygial foramen left dorsolateral but almost basal in position; hypandrium simple; aedeagus simple, with internal appendix; epandrial seta positioned distad, near epandrial lobes; pedicels of epandrial lobes absent, with the 2 bristles of lobes arising directly from epandrium, distal bristle much stronger than basal bristle; surstylus fused to epandrium, bent, with single capitate arm which bears distinctive ventral striated projection and various strong curved apical setae; cercus fused medianly, and with short distolateral projection which bears short apical setal projection.

Female: similar to male but lack MSSC.

Remarks. *Medetera melanesiana* is known from New Guinea, the Solomon Islands, and Cape York Peninsula, Queensland.

Medetera kokodensis n. sp.

Type material. HOLOTYPE ♂: **Papua New Guinea:** Kokoda-Pitoki, 400 m, 23 March 1956, J.L. Gressitt (BPBM)

Description. Male: length 2.0; wing dimensions 1.9 x 0.7; similar to *M. melanesiana* except as noted.

HEAD: vertex, frons, face and clypeus shining metallic violet.

LEGS: coxa I yellow, with some metallic green infuscation anteriorly; coxae II and III brown; femora yellowish; remainder of legs yellow; setae yellow.

ABDOMEN: entirely dark metallic green with bronze reflections, with dusting of grey pruinosity, and with short dark setulae; segment 7 not greatly elongated; hypopygium dark brown with yellowish cerci (Fig. 5c); epandrium flattened, subrectangular, elongate, with hypandrium arising from midventral position; hypopygial foramen left dorsolateral in position; hypandrium simple, relatively short; aedeagus simple, lacking internal appendix; epandrial seta strong, positioned distad, near epandrial lobes; pedicels of epandrial lobes absent, with the 2 bristles of lobes arising directly from epandrium; surstylus fused to epandrium, relatively short, with single capitate arm which bears 2 strong curved apical setae; cercus fused medianly, and with short deflexed distolateral projection.

Female: unknown.

Medetera morobensis n. sp.

Type material. HOLOTYPE ♂: **Papua New Guinea:** Wau, Morobe District, 1250 m, 13 Oct 1962, J. Sedlacek (BPBM). PARATYPES: ♂, 6♀♀, same location but with dates Jan, July, Sept, Oct, Nov, 1961–1963; ♂, **Indonesia:** Irian Jaya: Nabire, 5–50 m, 25 Aug to 2 Sept 1962 (BPBM).

Description. Male: length 2.3; wing dimensions 2.1 x 0.8; similar to *M. melanesiana* except as noted.

THORAX: dorsum shining metallic blue-violet with dusting of grey pruinosity; setae black; 6–7 pairs ac present.

LEGS: coxae and basal ⅔ of femora brown; remainder of legs yellow although TI sometimes infuscated and distal tarsomeres darkened; leg setae yellowish to brown.

ABDOMEN: entirely dark metallic green with bronze reflections, with dusting of grey pruinosity and short pale setulae; hypopygium dark brown with yellowish cerci (Fig. 5a–b); epandrium strongly flattened, subrectangular, elongate, with hypandrium arising from midventral position; hypopygial foramen left basolateral in position; hypandrium simple; aedeagus simple, lacking internal appendix; epandrial seta short, positioned adjacent to epandrial lobes; pedicels of epandrial lobes weakly developed but

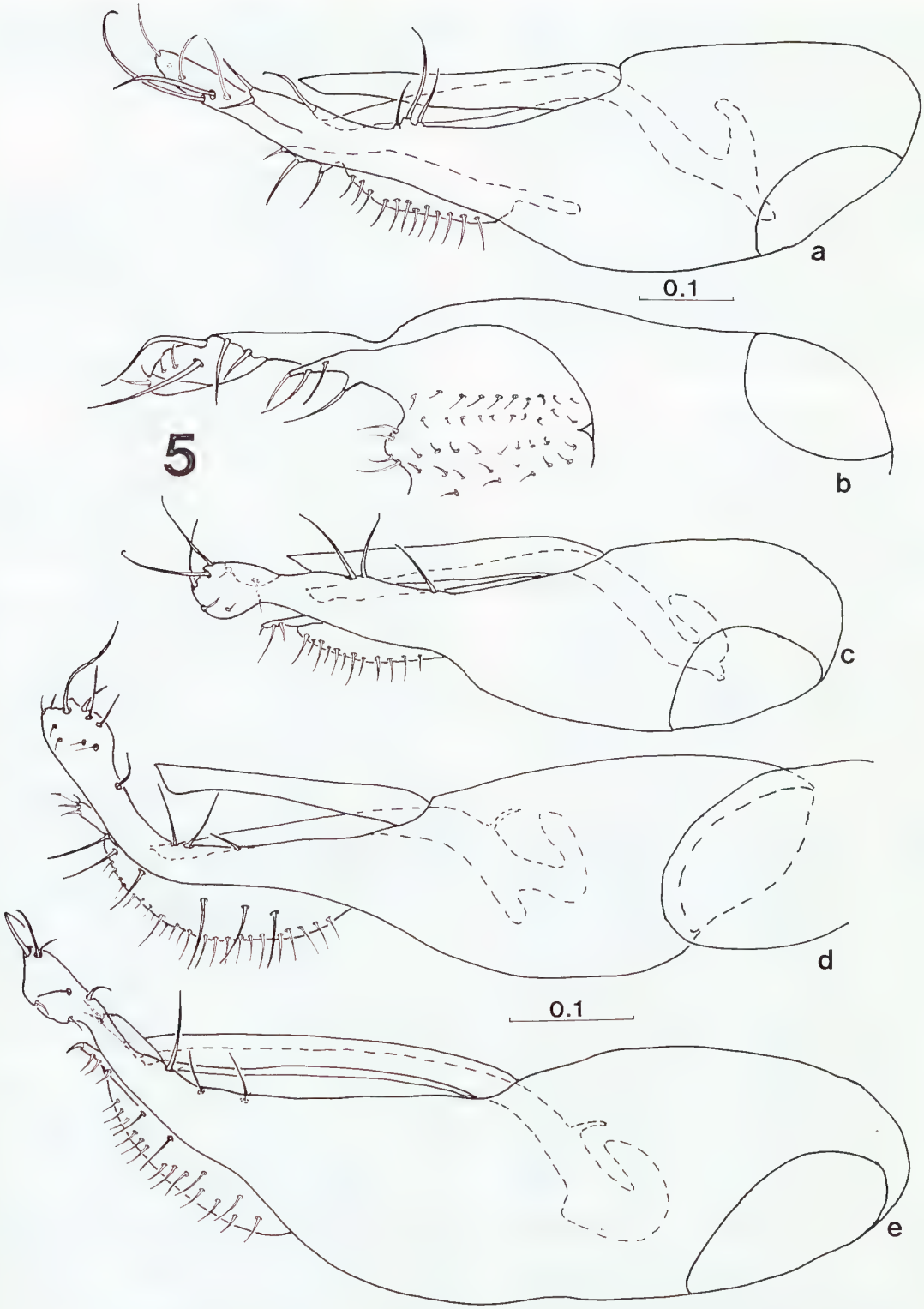

Fig. 5. a–b, *M. morobensis,* Wau, Papua New Guinea; a, hypopygium, left lateral view; b, left hypopygium, dorsal view. **c,** *M. kokodensis,* Kokoda, Papua New Guinea; hypopygium, left lateral view. **d,** *M. niuginiensis,* Mt Hagen, Papua New Guinea; hypopygium, left lateral view. **e,** *M. melanesiana* New Britain; hypopygium, left lateral view.

present, with bristle of basal lobe longer than that of distal lobe; surstylus fused to epandrium, ventral arm of surstylus evident overlapping longer dorsal arm; dorsal surstylar arm not capitate and bearing some strong curved distal setae; cercus fused medianly, and with short distolateral projection which bears apical seta, 2 strong dorsal setae, and curved peduncluate median seta.

Female: similar to male but lacks long pale anteroventral setae of FIII.

Remarks. *Medetera morobensis* is known only from New Guinea. It retains some plesiomorphic characters with respect to other members of the *melanesiana* group, in particular, the presence of short peduncular bases on the epandrial lobe and the remnant of the ventral surstylar arm.

Medetera niuginiensis n. sp.

Type material. HOLOTYPE ♂: **Papua New Guinea:** West Highlands, Hagen, south-east of Koinfam, 15 Oct 1958, J.L. Gressitt (BPBM). PARATYPES: 2♂♂, Wau, 1250 m, 20 May 1965 (BPBM); ♂, Brown River, near Port Moresby, 21 Oct 1963 (AMS).

Additional material. Possible ♀: **Papua New Guinea:** West Highlands, Baiyer River, 1200 m, 5 Aug 1982 (PDPI).

Description. Male: length 2.3; wing dimensions 2.1 x 0.8; similar to *M. melanesiana* except as noted.

THORAX: dorsum shining metallic blue-violet with dusting of grey pruinosity; setae black; 6–7 pairs ac.

LEGS: coxae and basal ⅔ of femora brown; remainder of legs yellow although TI sometimes infuscated and distal tarsomeres darkened; setae yellowish.

ABDOMEN: dark metallic green with bronze reflections, with dusting of grey pruinosity, and with short pale setulae; distal half of segments 6–8 and basal portion of epandrium pale cream and weakly sclerotized in specimens from Wau (see Remarks); hypopygium dark brown with yellowish cerci (Fig. 5d); epandrium strongly flattened, subrectangular, elongate, with hypandrium arising from midventral position; hypopygial foramen left basolateral in position; hypandrium simple; aedeagus simple, with internal appendix; epandrial seta short, positioned distad, near epandrial lobes; pedicels of epandrial lobes absent, with 2 subequal bristles of lobes arising directly from epandrium; surstylus fused to epandrium, strongly curved ventrally, relatively short, with single capitate arm which bears various strong curved apical setae; cercus fused medianly, and with short distolateral projection.

Female: similar to male but lacks MSSC; abdomen entirely metallic green.

Remarks. *Medetera niuginiensis* is known only from New Guinea, especially the Highlands area. The males from Wau only had the distal half of segments 6–8 and basal portion of epandrium pale cream and weakly sclerotized. In all other respects, however, their hypopygia were identical to those of the other males. The development of a weakly sclerotized and melanized male postabdomen is also found in *M. rhetheura* and in *M. macalpinei.*

Medetera macalpinei n. sp.

Type material. HOLOTYPE ♂: **Papua New Guinea:** Woitape, Wharton Range, 20 Oct 1963, D.K. McAlpine. PARATYPES: 2♂♂, same locality, 19 Oct 1963, 11 Oct 1963 (AMS); 2♂♂, Wau, 1250 m, 7–21 Aug 1965 (BPBM); 1♂, 1♀, Aiyura, East Highlands, 1800 m, 7 Jan 1964 (BPBM).

Additional material. 10♂♂, 11♀♀, **Australia:** Queensland, 4 km south-east of Kumbia, on *Eucalyptus* trunks, 10 April 1982 (ANIC).

Description. Male: length 2.0; wing dimensions 1.9 x 0.7; similar to *M. melanesiana* except as noted.

THORAX: setae yellowish to dark brown.

LEGS: coxae basally brown, distally yellowish to infuscated; femora yellowish to infuscated brownish; remainder of legs yellow although distal tarsomeres darkened; leg setae yellowish; relative podomere ratios similar; FIII with anterior and anteroventral rows of setae, the anteroventral row particularly long (Fig. 6e) (MSSC).

ABDOMEN: basally dark metallic green with bronze reflections, with dusting of grey pruinosity, and with short pale setulae; distal half of segments 6–8 and basal portion of epandrium pale cream colour and weakly sclerotized (MSSC); hypopygium dark brown distally with yellowish cerci (Fig. 6a–d); epandrium strongly flattened, subrectangular, basally truncate, with hypandrium arising from midventral position; hypopygial foramen left basolateral in position; hypopygial foramen basal, only slightly left lateral in position; aedeagus simple, with internal appendix; epandrial seta positioned distad, near basal epandrial lobe; pedicels of epandrial lobes absent, with 2 subequal bristles of lobes arising directly from epandrium; surstylus fused to epandrium, relatively short, with single capitate arm which bears various strong curved apical setae; cercus fused medianly, and with short distolateral projection which bears strong short apical seta.

Female: similar to male but without MSSC; abdomen entirely metallic green.

Remarks. *Medetera macalpinei* is known from New Guinea and south-eastern Queensland. The distal half of segments 6–8 and the basal portion of epandrium are pale cream colour and weakly sclerotized in all specimens. There is some variation in the development of the surstylus and the arrangment of the curved surstylar setae (Fig. 6a–c). Even the holotype and paratype from Woitape, New Guinea, show marked differences in the distal surstylus. For this reason, the specimens from Kumbia, Queensland, in rather semiarid country near the Bunya Mountains, were considered conspecific even though the distal surstylus differed

somewhat from that of the holotype. Coxa I and the femora of the Kumbia specimens are also somewhat paler than those of the New Guinea specimens. However, all male specimens have the elongate ventral setae on FIII.

Medetera rhetheura n. sp.

Type material. HOLOTYPE ♂, PARATYPES 7♂♂, 2♀♀: **Papua New Guinea:** Korogo, Sepik River, 10 March 1964, D.H. Colless (ANIC).

Additional material. Indonesia: Irian Jaya: 2♂♂, 1♂, Nabire, south of Geelvinck Bay, 5–50 m, 25 Aug to 2 Sept 1962. **Papua New Guinea:** 1♂, Wau, 1250 m, 20 Aug 1965; 1♂, Daradae, 80 km north of Port Moresby, 80 m, 5 Sept 1959; 1♂, south-east Murua River, 10 m, 20 Dec 1964; 6♀♀, either *M. rhetheura* or *M. melanesiana:* Waghi Valley; Kerowagu; Wau, Morobe District; Sepik, Angoram; Eliptamin Valley, 1350–1665 m (all BPBM).

Description. Male: length 2.0; wing dimensions 1.9 x 0.7; similar to *M. melanesiana* except as noted.

LEGS: FIII with long pale ventral seta at ¼, about as long as entire femur (Fig. 6h) (MSSC).

ABDOMEN: dark metallic green with bronze reflections, with dusting of grey pruinosity, and with short pale setulae; distal half of segments 6–8 and basal portion of epandrium pale cream colour and weakly sclerotized, contrasting strongly with the preceeding segments; distal epandrium dark brown with yellow cerci (Fig. 6f–g); epandrium strongly flattened, basally bent, subrectangular, elongate, with

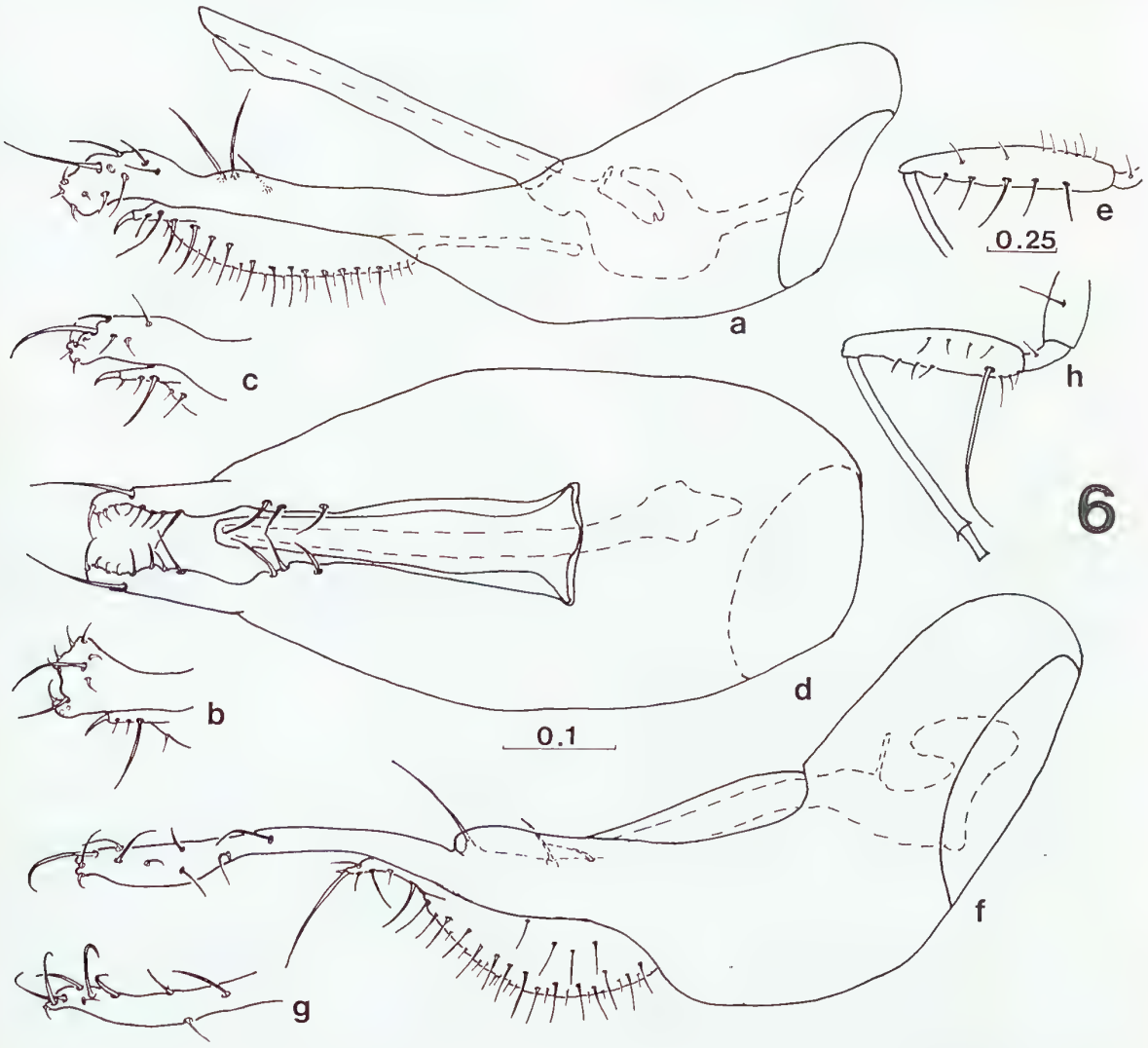

Fig. 6. a–e, *M. macalpinei;* a–b, Woitape, Papua New Guinea; **a,** holotype, hypopygium, left lateral view; **b,** paratype, surstylus and distal cercus, left lateral view. c–e, Kumbia, Queensland; **c,** surstylus and distal cercus, left lateral view; **d,** hypopygium, ventral view; **e,** basal right leg male, anterior view. **f–h,** *M. rhetheura;* **f,** Nabire, Irian Jaya; hypopygium, left lateral view. g-h, Sepik River, Papua New Guinea; **g,** surstylus, left lateral view; **h,** basal right leg male, anterior view.

hypandrium arising from midventral position; hypopygial foramen dorsobasal, only slightly left lateral in position; hypandrium simple; aedeagus simple, with internal appendix; lateral development of epandrium covers epandrial seta and epandrial lobes in lateral view; epandrial seta positioned distad, near basal epandrial lobe; epandrial lobes well separated; surstylus fused to epandrium, greatly prolonged and narrow, with arms arched medianly, and with curved apical setae as figured; cercus fused medianly, and with short distolateral projection which bears long apical seta.

Female: similar to male but lacks long pale ventral seta of FIII and tooth-like projection of $IIIt_1$; abdomen entirely metallic green.

Remarks. *Medetera rhetheura* is known only from New Guinea. The elongate surstylus, cream coloured postabdomen and basal epandrium, and the long ventral seta of the male FIII are distinctive. Some variation exists in the configuration of the apical surstylar setae (Fig 6f–g). This species is closely related to *M. melanesiana,* and isolated females cannot be accurately separated.

The *chillcotti* Group

The *chillcotti* group is defined by the following features: small, less than 1.5 in length; Ac reduced to minute hairs; two strong dc, bordering mesonotal depression, anterior dc reduced to short setulae; lateral scutellars reduced to weak hairs; M not strongly curved anteriorly, but rising gradually toward R_{4+5} (as in Fig. 2i); surstylus fused to epandrium, without membranous connection; epandrial lobes separate, each bearing a strong bristle; surstylus divided into three arms; aedeagus not recurved within epandrium; hypandrium simple, subrectangular; cercus with dorsoapical blade-like seta; cercus with distinctive ventral setose protuberance.

The *chillcotti* group comprises two closely related species, *Medetera chillcotti* and *M. bishopae,* and has an Oriental distribution. This group is not characterized by any strong autapomorphy. In cercal and surstylar structure it seems closely allied to *M. vivida* of the *toxopeusi* group, but lacks the distinctive recurved aedeagus.

From Becker's description, *M. adsumpta* from India might belong to this group.

Medetera bishopae n. sp.

Type material. HOLOTYPE ♂: **Malaysia:** West Malaysia: Fraser's Hill, 1300 m, 16 March 1966, J. Sedlacek. PARATYPES: ♀, Pahang Kuala Tahan, 12–14 Dec 1958; ♂, Sabah: Sandakan Bay (SW), Sapagaya Lumber Camp, 2–20 m, 5 Nov 1957 (all BPBM).

Description. Male: length 1.3; wing dimensions 1.2 x 0.5.

HEAD: vertex, frons, face, clypeus dark metallic green with grey pruinosity; proboscis dark brown; antenna black; arista very long, more than twice the head height.

THORAX: dorsum metallic green, posterior portion of mesonotum brownish; pleura covered with dense grey pruinosity; setae yellowish.

LEGS: coxae and basal half of femora brown; remainder of legs yellow; relative podomere ratios as I: 1.1; 1.1; 0.3/0.3/0.2/0.1/0.1; II: 1.2; 1.4; 0.5/0.3/0.2/0.1/0.1; III: 1.5; 1.8; 0.3/0.6/0.3/0.2/0.1.

WING: similar to Fig. 2i; CuAx ratio 0.3; lower calypter yellow with fan of pale setae; haltere yellow.

ABDOMEN: metallic green with some grey pruinosity; hypopygium dark brown with yellowish cerci (Fig. 7b); hypandrium and aedeagus elongate, simple; epandrial seta positioned adjacent to epandrial lobes; pedicel of distal epandrial lobe more than twice length of basal lobe; middle surstylar arm bearing strong lateral seta; ventral surstylar arm narrow with apical seta; cercus with apical seta, and with tapering ventral projection which bears strong distal seta and 3 somewhat weaker setae on proximal side.

Female: similar to male.

Remarks. *Medetera bishopae* is found on the Malay Peninsula and Borneo, and is named after Bernice P. Bishop, benefactor of the Bishop Museum.

Medetera chillcotti n. sp.

Type material. HOLOTYPE ♂, PARATYPE ♂: **Nepal:** Lothar, near Birganji, 138 m, malaise trap, 17 Sept 1967, Canadian Nepal Expedition (CNC).

Description. Male: length 1.4; wing dimensions 1.4 x 0.5.

HEAD: vertex, frons, face, clypeus black with metallic blue reflections, and covered with dense brown pruinosity; proboscis black; antenna black; arista about 1 ½ times as long as head height.

THORAX: black with metallic blue reflections and covered with dense grey-brown pruinosity; setae brownish.

LEGS: coxae brown, with coxa I yellowish laterally; remainder of legs entirely yellow with only distal tarsomeres darkened; podomere ratios as in *M. bishopae.*

WING: similar to Fig. 2i; CuAx ratio 0.3; lower calypter and haltere yellow.

ABDOMEN: dark brown with metallic blue reflections, and with short yellowish setulae; hypopygium dark brown with yellowish cerci (Fig. 7a); hypandrium and aedeagus simple; epandrial lobes with short collar-like bases; surstylus divided into 3 arms which are curved mediad, and bearing setae as figured; cercus with dorsoapical blade-like seta and capitate ventral prominance bearing 4 strong setae.

Female: unknown.

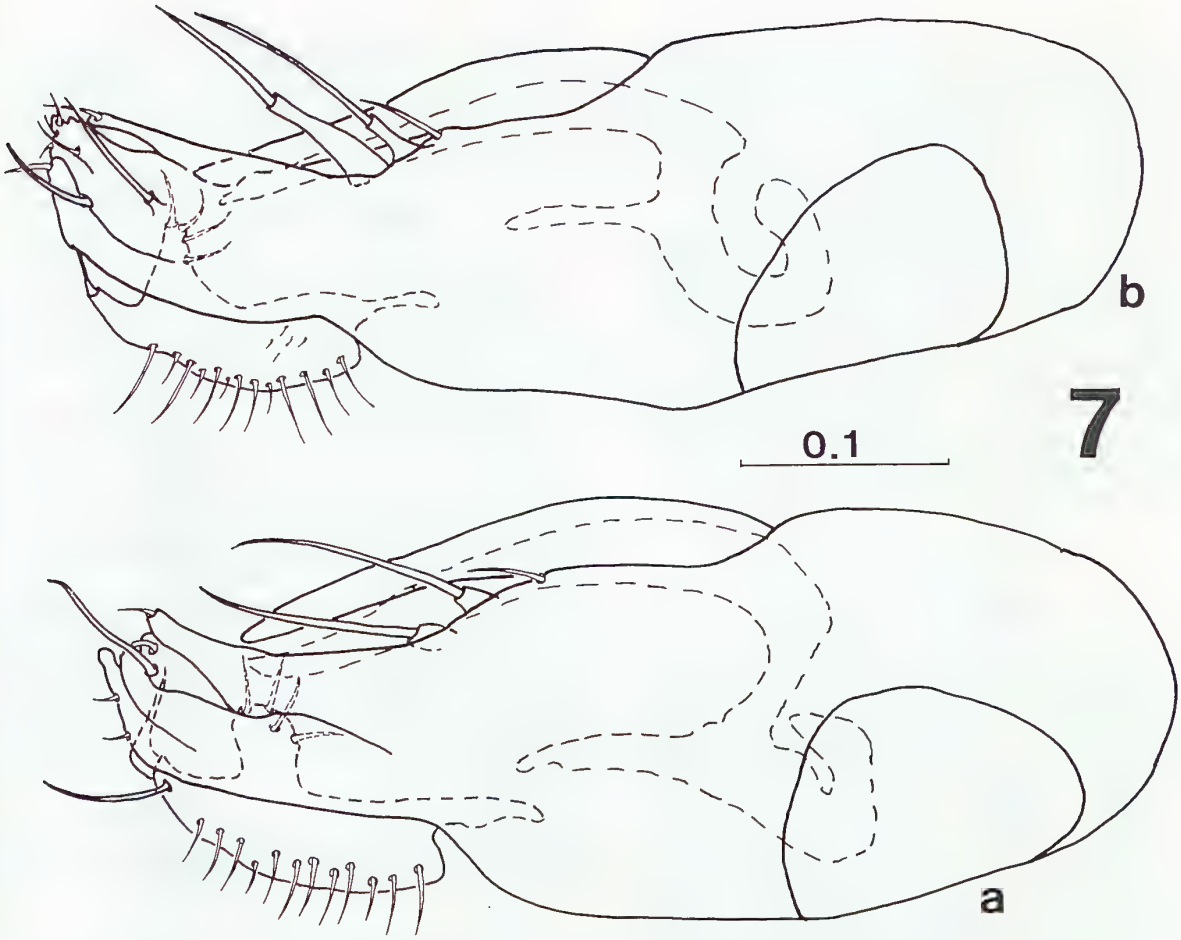

Fig. 7. a, *M. chillcotti*, Nepal; hypopygium, left lateral view. b, *M. bishopae*, Kedah, Malaysia; hypopygium, left lateral view.

Remarks. *Medetera chillcotti* is known only from lowland Nepal and is named after the dipterist J.G. Chillcott, who died while on the Canadian Nepal Expedition. This species and *M. bishopae* have similar hypopygia.

The *australiana* and *toxopeusi* Groups

The *australiana* and *toxopeusi* groups both share the following features: proboscis keel-like and projecting anteriad; two strong dc bordering mesoscutal depression, the anterior dc reduced to short setulae; epandrium elongate and cylindrical, and distance between distal epandrial lobe and hypandrial base greater than distance between hypandrial base and base of epandrium; epandrial lobes positioned distad, such that the distalmost lobe is adjacent to the join of the surstylus with the epandrium; hypandrium elongate, subrectangular; aedeagus strongly recurved within the epandrium, extending far basad within the epandrium before curving back on itself and forming the ejaculatory bulb (e.g., Figs 8, 9) (synapomorphy for the two groups); surstylus usually with membranous attachment to epandrium; surstylus usually deeply cleft.

The *australiana* group has the following features: antenna entirely black; arista length approximately equal to head height; pleura and coxae with grey or bright silvery pruinosity; lateral scutellars about ¾ length of median scutellars; coxae and basal ⅔ of femora black; cercus relatively simple, tapering or blunt, without apical modified setal projections.

The *australiana* group includes four species from the eastern coasts and ranges of Australia which, as distinguished in the key, can be divided into two pairs of closely related species, *Medetera australiana* and *M. mosmanensis*, and *M. queenslandensis* and *M. wongabelensis*.

The *toxopeusi* group has the following features: scape and pedicel usually yellow, and 1st flagellomere black; arista relatively long, usually greater than twice head height; scutellum, posterior mesonotum and

postpronotum often appearing yellow-brown, in contrast to the general darker metallic colouration of the thorax; lateral scutellars usually less than ½ length of median scutellars; bristle of the distal epandrial lobe often with hair-like branches; epandrial seta positioned distad along ventral epandrial margin; cercus often with distinctive ventral lobes and/or setae, and usually with modified apical seta.

The *toxopeusi* group comprises 7 species, all except *M. vivida* from the Papuan region east of Weber's Line. *Medetera toxopeusi, M. waris, M. papuensis* and *M. cheesmanae* are closely related with similar hypopygia and body colouration. *Medetera vivida* and *M. gressitti* have an unbranched distal surstylar bristle, and entirely metallic green thorax. *Medetera irianensis* appears somewhat isolated, lacking both a deep surstylar cleft and modified cercal setae, and in having the surstylus fused to the epandrium.

The *australiana* Group

Medetera mosmanensis n. sp.

Type material. HOLOTYPE ♂ (ANIC), PARATYPES ♂, 3♀♀: **Australia:** New South Wales: Mosman, Ashton Park, on trunks of *Angophora costata,* 12 Oct 1980, D. J. Bickel. PARATYPES: ♂, same except 12 Feb 1984; 8♂♂, 4♀♀, Mosman, Balmoral Beach, on trunks of *Ficus macrophylla,* 21 Sept to 15 Nov 1980 (paratypes AMS, ANIC).

Description. Male: length 2.5–2.7; wing dimensions 2.7 x 0.8.

HEAD: vertex, frons metallic green-black with bronze reflections and covered with some brown pruinosity; face, clypeus bright satiny metallic blue-green with some pruinosity laterally and on frontoclypeal suture; proboscis black, massive.

THORAX: dorsum dark metallic green with bronze reflections, with brown pruinosity dorsally and grey pruinosity on pleura and coxae; setae black; 8–10 pairs ac about as long as width of ac band.

LEGS: coxae, basal ⅔ of femora black with grey pruinosity; distal femora, remainder of legs yellow to infuscated red-brown; podomere ratios as: I: 2.6; 2.3; 0.9/0.9/0.5/0.3/0.3; II: 2.8; 2.7; 1.4/1.0/0.6/0.4/0.2; III: 2.7; 3.1; 0.5/1.5/0.8/0.4/0.4.

WING: M gradually approaches R_{4+5} (Fig. 2h); CuAx ratio 0.6; lower calypter yellow with brown rim and fan of pale setae; haltere yellow.

ABDOMEN: metallic black-bronze with short black setulae; hypopygium black with brownish cerci, elongate, cylindrical and somewhat dorsoventrally flattened (Fig. 8a); hypandrium elongate, forming an inverted trough over aedeagus; epandrial seta and epandrial lobes positioned far distad near junction between surstylus and epandrium; surstylus deeply cleft into dorsal and ventral arms; dorsal surstylar arm elongate with ventral subapical seta; ventral surstylar arm with a recurved striated seta and other setae as figured; cercus elongate, tapering.

Female: similar to male but with wider face.

Remarks. *Medetera mosmanensis* is known only from the Sydney district. Both *M. mosmanensis* and *M. australiana* have been collected off trunks of smoothbarked trees, and they are sympatric at least in the Sydney district.

Medetera australiana n. sp.

Type material. HOLOTYPE ♂, PARATYPES ♂, ♀, **Australia:** New South Wales: Coffs Harbour, on trunk *Eucalyptus* sp., 24 Oct 1980, D. J. Bickel (ANIC). PARATYPES: 2♂, Mosman, Ashton Park, on trunks *Angophora costata,* 18 Oct 1980 (AMS); ♂, Mooney Mooney Creek, near Gosford, 18 Jan 1980 (AMS).

Description. Male: length 2.9–3.1; wing dimensions 3.0 x 0.8; similar to *M. mosmanensis* except as noted.

LEGS: coxae, femora black with grey pruinosity; remainder of legs dark brown to black.

WING: CuAx ratio 1.0; haltere yellow to reddish brown.

ABDOMEN: aedeagus in lateral view somewhat expanded apically (Fig. 8c); surstylus with membranous attachment to epandrium; dorsal surstylar arm clavate; ventral surstylar arm short, stout, curved, and with prominent setae as figured; cercus stout, apically curved with long subapical seta on ventral margin.

Female: similar to male.

Remarks. *Medetera australiana* ranges from the northern New South Wales coast to the Sydney district.

Medetera queenslandensis n. sp.

Type material. HOLOTYPE ♂: **Australia:** Queensland: Mt Tamborine, 20 March 1965, T. Weir (UQIC, deposited QMB). PARATYPE: ♂, New South Wales: Mt Warning National Park, on trunk *Archontophoenix cunninghamiana,* 24 Nov 1985 (AMS).

Description. Male: length 3.4; wing dimensions 3.1 x 1.1; similar to *M. mosmanensis* except as noted.

THORAX: bright metallic green-bronze reflections; pleura and coxae with pruinosity which appears bright silvery when viewed anteriorly.

LEGS: coxae and basal ⅔ of femora black with silvery pruinosity; reminder of legs yellow.

WING: CuAx ratio 0.7.

ABDOMEN: hypopygium elongate, cylindrical (Fig. 8d); aedeagus with subapical triangular projection; epandrial seta short, positioned midway between base of hypandrium and distal epandrial lobe; surstylus with membranous attachment to epandrium; dorsal surstylar arm keel-shaped with strong lateral seta; ventral surstylar arm with prominence bearing 2 strong setae, and tapering distally with apical stout seta; cercus with blunt apex.

Female: unknown.

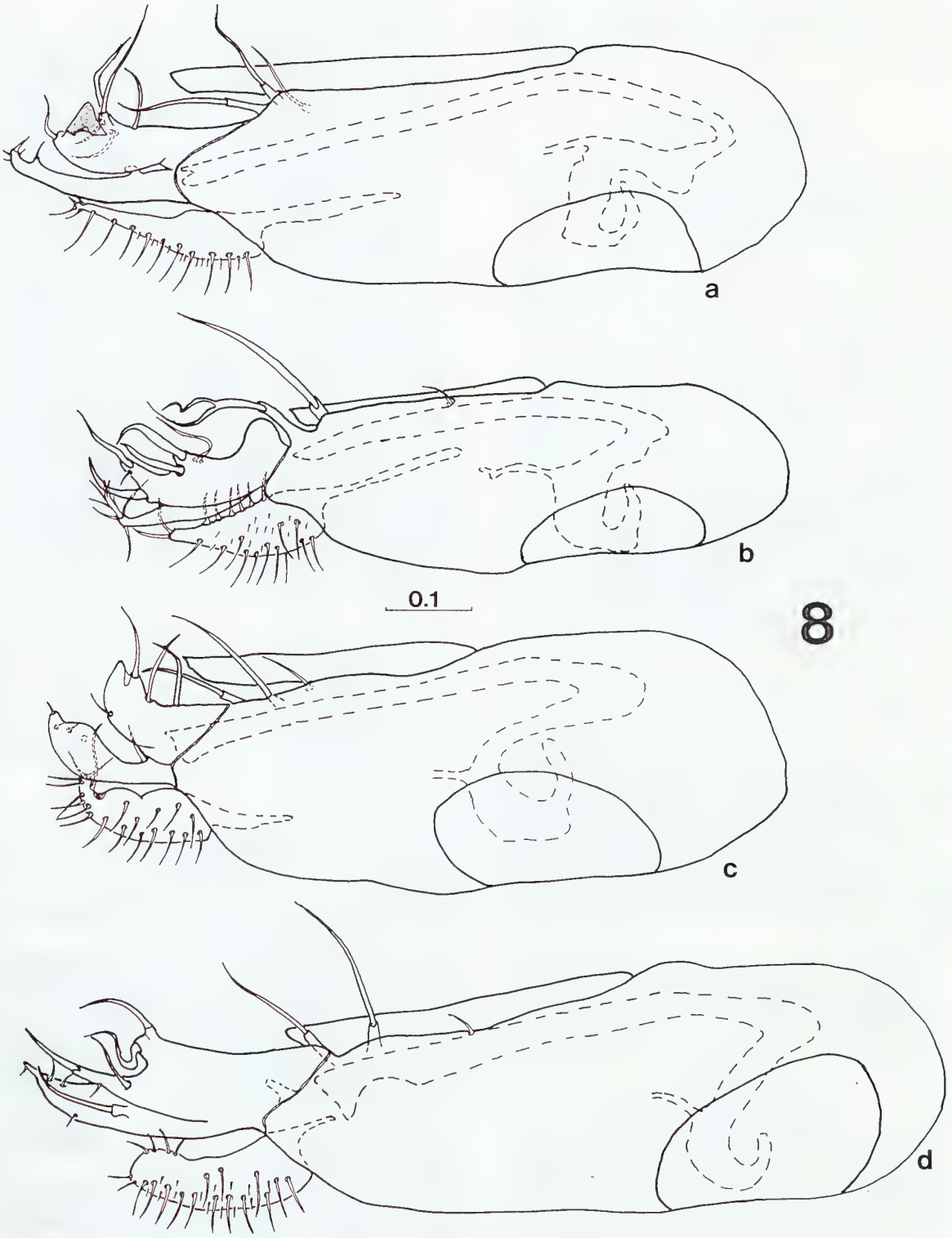

Fig. 8. a, *M. mosmanensis,* Mosman, New South Wales; hypopygium, left lateral view. **b,** *M. wongabelensis,* Atherton, Queensland; hypopygium, left lateral view. **c,** *M. australiana,* Coffs Harbour, New South Wales; hypopygium, left lateral view; **d,** *M. queenslandensis,* Mt Tamborine, Queensland; hypopygium, left lateral view.

Remarks. *Medetera queenslandensis* is known from south-eastern Queensland and north-eastern New South Wales. This species is relatively large in comparison with other members of the *australiana* group.

Medetera wongabelensis n. sp.

Type material. HOLOTYPE ♂: **Australia:** Queensland: Wongabel State Forest, near Atherton, 17°20′S 145°31′E, at light, 18 Nov 1981, D. H. Colless (ANIC).

Description. Male: length 2.6; wing dimensions 2.3 x 1.0.

HEAD: vertex, frons, face metallic blue-black with grey pruinosity; clypeus satiny metallic blue; proboscis black.

THORAX: dorsum dark metallic green with bronze reflections and covered with brown pruinosity dorsally; pleura and mesonotal depression covered with dense silvery pruinosity, evident in anterior view; setae black; 8–10 pairs ac, increasing in length posteriorly.

LEGS: coxae, basal ⅔ of femora black with silvery pruinosity, remainder of legs yellowish with distal tarsomeres darkened; podomere ratios similar to *M. mosmanensis;* It_{1-3} with bright anterior silvery hairs on the basal ½ to ⅔ of each tarsomere, thus giving appearance of 3 silvery patches separated by darker integument (probably MSSC); TIII with pale preapical dorsal seta.

WING: CuAx ratio 0.6; lower calypter yellow with fan of pale setae; haltere yellow.

ABDOMEN: black with metallic green-bronze reflections; short black setulae; hypopygium elongate, cylindrical, and black with yellowish cerci (Fig. 8b); epandrial seta short, positioned midway between epandrial lobes and base of hypandrium; distal epandrial lobe with forked bristle; surstylus with membranous attachment to epandrium; dorsal surstylar arm with distinctive subapical branched seta; ventral surstylar arm with strong setae as figured; cercus tapering with apical seta and ventral row of 5 setae.

Female: unknown.

Remarks. The patches of silvery hairs on tarsomeres 1–3 on leg I are probably a male secondary sexual character.

The *toxopeusi* Group

Medetera waris n. sp.

Type material. HOLOTYPE ♂: **Indonesia:** Irian Jaya: Waris, south of Hollandia, 450–500 m, 8–15 July 1959, T. C. Maa (BPBM).

Description. Male: length 3.2; wing dimensions 2.9 x 1.0.

HEAD: vertex, frons, face and clypeus metallic bluegreen with grey pruinosity; proboscis brown, massive, protruding keel-like; scape and pedicel yellow; 1st flagellomere brown.

THORAX: metallic green with grey pruinosity; rim of scutellum brown; ac short, less than width of ac band; lateral scutellars less than ⅓ length of medians.

LEGS: coxa I yellow; coxae II and III brown; remainder of legs yellow; podomere ratios as: I: 2.7; 2.6; 1.0/1.0/1.0/0.5/0.4; II: 2.7; 2.6; 1.7/1.4/1.0/0.5/0.4; III: 3.0; 3.3; 0.8/2.0/1.1/0.5/0.4.

WING: M gradually approaches R_{4+5}; CuAx ratio 0.5; lower calypter yellow with fan of pale setae; haltere yellow.

ABDOMEN: metallic green with bronze reflections and short black setulae; hypopygium dark brown with yellowish cerci (Fig. 9b); hypandrium elongate, tapering distally; aedeagus strongly recurved within epandrium and tapering distally; distal epandrial lobe with plumose bristle; surstylus with membranous attachment to epandrium; dorsal surstylar arm long, extending beyond ventral arm; ventral surstylar arm with V-shaped cleft and with setae as figured; cercus apically clavate and bearing ventrally directed blade-like seta; plumose setal projection borne medioventrally on cercus, other setae as figured.

Female: unknown.

Remarks. See below under *M. toxopeusi.*

Medetera toxopeusi Parent

Medetera toxopeusi Parent, 1932b: 352.

Type material. HOLOTYPE ♂: **Indonesia:** Maluku: Buru Island, Station 9, 21 May 1921, L. J. Toxopeus (ZMUA, examined).

Description. Male: length 2.5; wing dimensions 2.6 x 0.95; similar to *M. waris* except as noted.

THORAX: anterior mesonotum, lower pleura metallic blue-green; posterior mesonotum including depression, humeral area, upper pleura, metapostnotum and scutellum brown yellow.

WING: CuAx ratio 0.3.

ABDOMEN: metallic green with grey pruinosity; hypopygium similar to *M. waris* except for details of surstylus (Fig. 9c); dorsal surstylar arm with some apical setae; ventral surstylar arm with deep V-shaped cleft, ventrally bearing flattened curved setae, and dorsally with strong tapering apical seta.

Female: unknown.

Remarks. *Medetera toxopeusi* and *M. waris* are very closely related species, exhibiting the same complex cercal structure. They are possibly conspecific, differing primarily in size and surstylar structure. The yellowish thoracic colouration of *M. toxopeusi* may reflect a teneral condition. However, such a pattern is also found in *M. cheesmanae* and widely in the *flaviscutellum* and *gracilis* species groups, and is possibly the mature colouration.

Medetera cheesmanae n. sp.

Type material. HOLOTYPE ♂, PARATYPES 1♂, 1♀: **Papua New Guinea:** Kokoda, 60 m, Sept to Oct 1933, L. E. Cheesman (BMNH). PARATYPES: 2♂♂, 1♀: Wau, 1050–1230 m, June, Oct, Nov 1965 (BPBM); 1♂, **Solomon Islands:** Guadalcanal, Roroni, 35 km east of Honiara, 12 May 1964 (BPBM).

Description. Male: length 1.9–2.0; wing dimensions 2.0 x 0.7; similar to *M. waris* except as noted.

THORAX: light brown with metallic green reflections on mesonotum and metapostnotum; pleura brownish with some grey pruinosity; scutellum mostly yellow; lateral scutellars about ½ length of medians.

WING: CuAx ratio 0.4.

ABDOMEN: dark brown with dusting of grey pruinosity; hypopygium brown with yellowish cerci (Fig. 9a); hypandrium elongate, tapering; epandrial seta strong; proximal epandrial lobe with long bristle, distal epandrial lobe with plumose bristle; surstylus with membranous attachment to epandrium; dorsal surstylar arm tapering with apical spatulate seta; ventral surstylar arm distally U-shaped with setae as figured; cercus with distinctive large subapical blade-like seta and setabearing cuticular projection on ventral surface, other setae as figured.

Female: similar to male except somewhat larger, body length 2.2–2.3.

Remarks. The colouration of the anterior mesonotum varies from light brown to a light metallic green with only the humeral area remaining brown. The thorax may become increasingly metallic coloured with age. *Medetera cheesmanae* is distributed from eastern New Guinea to the Solomon Islands.

Medetera papuensis n. sp.

Type material. HOLOTYPE ♂: **Papua New Guinea:** Central Province, Daradae, near Javarera, Aieme River, 100 m, 3 Oct 1958, J. L. Gressitt (BPBM).

Description. Male: length 1.8; wing dimensions 1.7 x 0.6; similar to *M. waris* except as noted.

HEAD: vertex, frons, face, clypeus black with green reflections, and covered with grey pruinosity; arista very long, more than twice head height.

THORAX: dorsum dark metallic green with bronze reflections and covered with grey pruinosity.

LEGS: all coxae and legs yellow.

WING: CuAx ratio 0.4.

ABDOMEN: dark brown with metallic green reflections and dusting of grey pruinosity; hypopygium brown with yellowish cerci (Fig. 9d); epandrial seta strong; proximal epandrial lobe with long bristle, distal epandrial lobe with plumose bristle; dorsal surstylar arm with long seta arising midmedianly and apical rectangular cuticular projection; ventral surstylar arm cleft with setae as figured; cercus with distinctive thin apical seta, other setae and projections as figured.

Female: unknown.

Medetera irianensis n. sp.

Type material. HOLOTYPE ♂, PARATYPE 1♀: **Indonesia:** Irian Jaya, Nabire, 5–50 m, malasie trap, 25 Aug to 2 Sept 1962, J. Sedlacek (BPBM) (both specimens badly rubbed).

Description. Male: length 1.6; wing dimensions 1.6 x 0.7; similar to *M. waris* except as noted.

HEAD: vertex, frons, face, clypeus dark metallic green with grey pruinosity.

THORAX: metallic green with bronze reflections; setae missing from specimens.

LEGS: coxae and basal portion of femora brown; distalmost femora and remainder of legs yellow; leg I missing but podomere ratios of legs II and III similar to *M. waris*.

WING: CuAx ratio 0.4.

ABDOMEN: black with metallic green reflections; hypopygium brown with yellowish cerci (Fig. 9e); epandrial seta and both epandrial lobes with elongate basal collars, and distal epandrial lobe bristle apically branched; surstylus fused to epandrium; surstylus with only shallow indentation separating dorsal and ventral arms; dorsal surstylar arm prolonged, curved, and capitate; surstylar setae as figured; cercus tapering and curved distally, with short apical setae.

Female: similar to male.

Medetera vivida Becker

Medetera vivida Becker, 1922: 51.

Type material. Becker described *Medetera vivida* from 1♂, 3♀♀ syntypes collected in Taiwan. I here designate the male, bearing the label "Formosa / Hoozan/ Sauter", as lectotype (DEI, examined).

Additional material. 1♂, **Indonesia:** Java, Tjibodas, 20 Sept 1958. 1♂, **Laos:** Vientiane Province, Ban Van Eue, 15–31 May 1965. 1♂, 1♀, **Singapore:** 4 June 1985 (CED). 1♂, **Taiwan:** Chiayi Chiayi Hsien, 12–13 April 1965 (all BPBM except where noted).

Description. Male: length 1.6; wing dimensions 1.6 x 0.7.

HEAD: vertex, frons, face, and clypeus black with metallic green reflections, and with grey pruinosity except clypeus; proboscis and antenna black; arista about as long as head height.

THORAX: dorsum shiny metallic green with dusting of grey pruinosity; setae yellowish; ac about as long as width of ac band; lateral scutellars about ½ length of medians.

LEGS: coxae and basal half of femora brown, remainder of legs yellow; podomere ratios as: I: 1.6; 1.5; 0.7/0.3/0.2/0.2/0.1; II: 2.0; 1.9; 1.0/0.4/0.3/0.2/0.2; III: 2.1; 2.3; 0.5/1.0/0.4/0.3/0.2.

WING: M gradually approaches R_{4+5}; CuAx ratio 0.4; lower calypter yellow with distinct brown rim

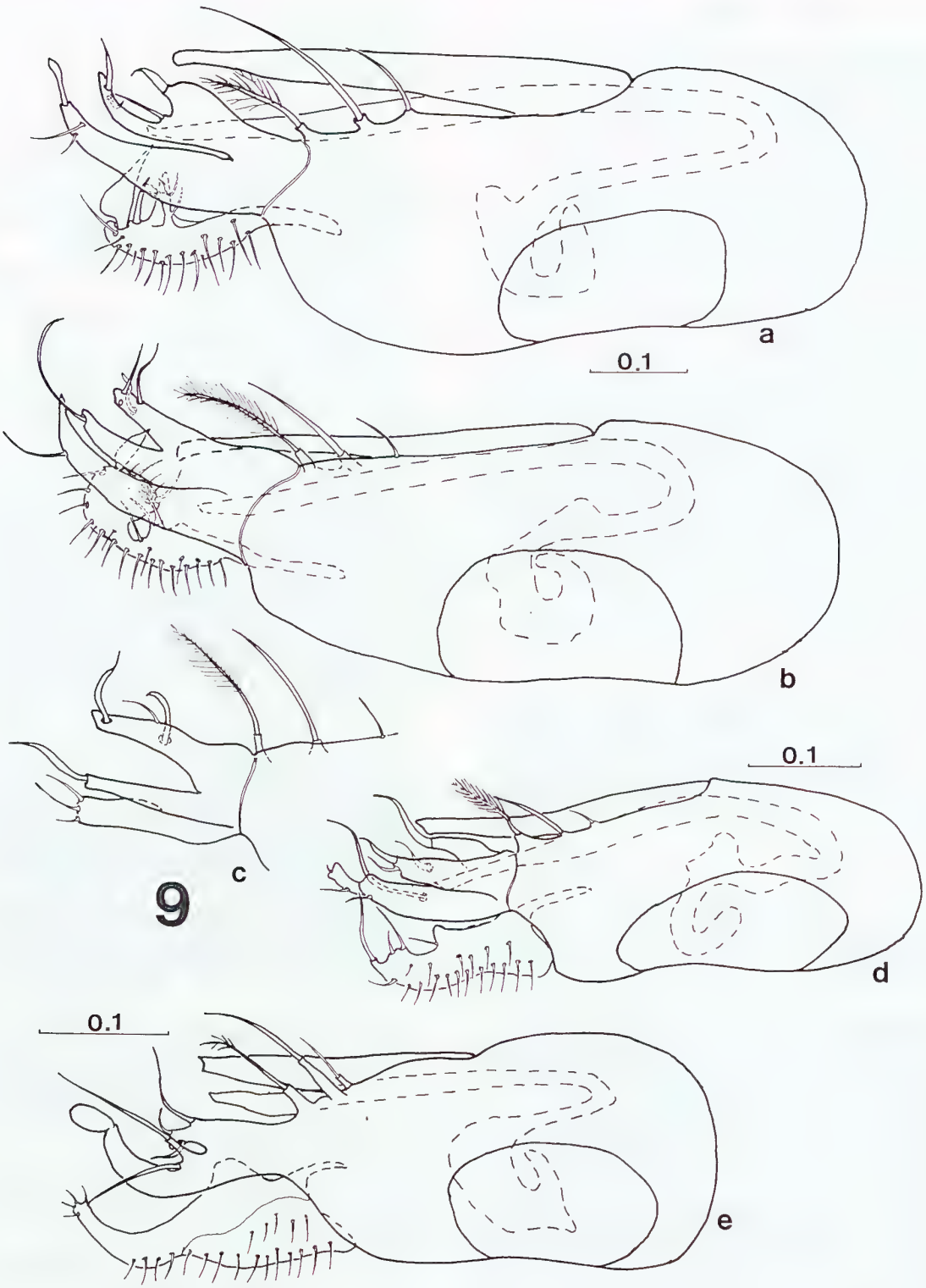

Fig. 9. a, *M. cheesmanae,* Kokoda, Papua New Guinea; hypopygium, left lateral view. **b,** *M. waris,* Waris, Irian Jaya; hypopygium, left lateral view. **c,** *M. toxopeusi,* Malku, Indonesia; surstylus, left lateral view. **d,** *M. papuensis,* Musgrave River, Papua New Guinea; hypopygium, left lateral view. **e,** *M. irianensis,* Nabire, Irian Jaya; hypopygium, left lateral view.

and fan of pale setae; haltere yellow.

ABDOMEN: metallic green with bronze reflections, and with short yellowish setulae; hypopygium dark brown with yellowish cerci (Fig. 10a–b); aedeagus with dorsoapical lobe and strongly recurved within epandrium; epandrial seta long, positioned midway between epandrial lobes and base of hypandrium; epandrial lobes each bearing strong simple bristle; surstylus with only weak suture marking attachment to epandrium; surstylus with cuticular projections and setae as figured; cercus ventrally with distinctive pilose capitate knob with blade-like seta at base which is partially obscured by lobate projection; cercus with strong apical curved blade-like seta.

Female: similar to male.

Remarks. *Medetera vivida* is distributed across southeastern Asia, from Taiwan and Indochina to Indonesia. The capitate knob of the cercus is distinctive.

Medetera gressitti n. sp.

Type material. HOLOTYPE ♂: **Papua New Guinea:** Kokoda-Pitoki, 400 m, 23 March 1956, J. L. Gressitt. PARATYPE: ♀, Kokoda, 28–29 March 1956 (BPBM).

Description. Male: length 1.6; wing dimensions 1.7 x 0.6.

HEAD: vertex, frons metallic green covered with grey pruinosity; face, clypeus metallic blue-green; proboscis black; scape and pedicel yellowish; 1st flagellomere black; arista about as long as head height.

THORAX: dorsum dark metallic green with bronze reflections; pleura with dense grey pruinosity; setae black; ac about as long as width of ac band; lateral scutellars reduced to weak hairs.

LEGS: coxae, femora brown; femoral 'knees' and remainder of legs yellow; podomere ratios as: I: 1.6; 1.4; 0.3/0.2/0.2/0.1/0.1; II: missing; III: 1.6; 1.9; 0.3/0.9/0.4/0.3/0.2.

WING: M gradually approaching R_{4+5}; CuAx ratio 0.3; lower calypter yellow with fan of pale setae; haltere yellow.

ABDOMEN: dark metallic green with short black setulae; hypopygium dark brown with yellowish cerci (Fig. 10c–e); hypandrium subrectangular; aedeagus tapering with pair of lateral processes; epandrial seta nearer to epandrial lobes than base of hypandrium; epandrial lobes positioned near membranous junction between surstylus and epandrium; lobate process arising from lateral wall of genital chamber present mediad of epandrial lobes; surstylus with ventral striae, arms, and setae as figured; cercus with curved blade-like apical seta, subtended by ventral mound bearing 4 strong setae.

Female: similar to male.

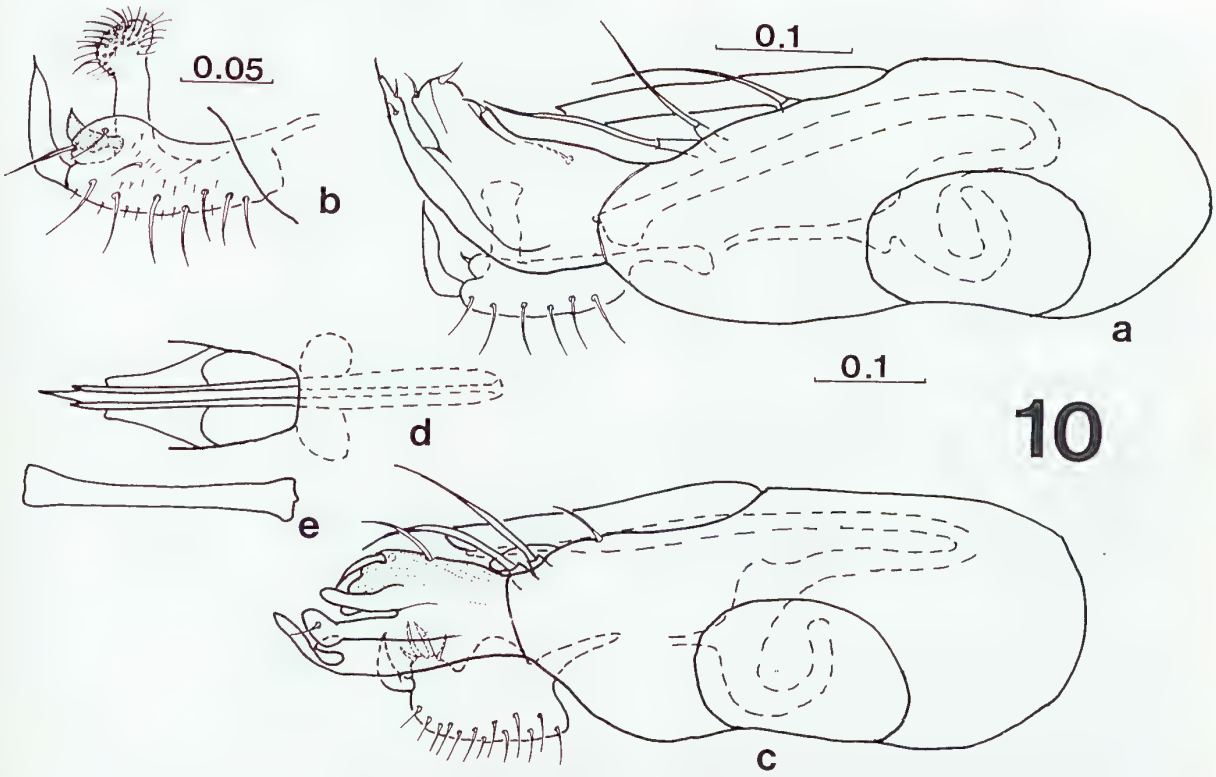

Fig. 10. a–b, *M. vivida,* Java; a, hypopygium, left lateral view; b, cercus, left lateral view. **c–e,** *M. gressitti,* Kokoda, Papua New Guinea; c, hypopygium, left lateral view; d, aedeagus, ventral view; e, aedeagus, ventral view.

The *gracilis* Group

The *gracilis* group is characterized by the following features: face shiny metallic blue-violet; tendency for posterior mesonotum to be yellow-brownish; ac reduced to absent (apomorphy); two strong dc bordering mesonotal depression, with the anterior dc much shorter and decreasing anteriorly; tendency for reduction and loss of posterior npl seta (apomorphy); lateral scutellars reduced to weak hairs, less than 1/10 length of stronger medians; silvery pruinose patches usually present on bodies of both sexes (apomorphy); tendency for prolongation of legs, with IIt_2 longer than IIt_1 and TII greater than FII in most species, also leg II longer than leg III (apomorphies); coxae I, legs mostly yellow; anal angle of wing reduced (Fig. 2e)(apomorphy).

The *gracilis* species group is confined to the Oriental tropics of Indonesia and Malaysia and includes four species: *M. gracilis, M. borneensis, M. sandakanensis* and *M. penangensis.*

The following tendencies are evident within the *gracilis* group, being best developed in *M. gracilis* itself: prolongation of the legs (with tarsomere 2 longer than tarsomere 1 on all legs), prolongation of the body with increased separation of coxa I and coxa II, and reduced anal angle of the wing (habitus figure in Hollis, 1964) (also, see Morphological Note 3).

Medetera borneensis n. sp.

Type material. HOLOTYPE ♂: **Malaysia:** Sabah (SE): Forest Camp, 19 km north of Kalabakan, 16 Nov 1962, K.J. Kuncheria (BPBM).

Description. Male: length 1.7; wing length x width 1.6 x 0.4.

HEAD: vertex, frons, metallic green with bronze reflections; upper half of face shiny metallic blue; lower half of face and clypeus dull coriaceous metallic greenbronze; proboscis somewhat weak, not strongly developed; scape and pedicel yellow; 1st flagellomere brownish; arista length about equal to 1½ head height.

THORAX: dorsum mostly metallic green with bronze reflections and with dusting of grey pruinosity; posterior portion of mesoscutum and scutellum brownish; setae black; ac short, less than width of ac band.

LEGS: entirely yellow, with only coxae II and III infuscated at bases; I: 1.6; 1.3; 0.5/0.4/0.3/0.3/0.2; II: 2.0; 1.9; 0.9/0.7/0.4/0.3/0.3; III: 1.6; 1.9; 0.4/0.8/0.4/0.3/0.2.

WING: ovate in shape with reduced anal angle, similar to Fig. 2e; CuAx ratio 0.3; lower calypter yellow with fan of pale setae; haltere yellow.

ABDOMEN: dark metallic green-bronze with short black setulae; hypopygium dark brown with yellow cerci (Fig. 11d); epandrium subrectangular; hypandrium trough-shaped, relatively short, only extending slightly beyond half-length of aedeagus; aedeagus elongate, apically upturned; epandrial seta short, near base of hypandrium; epandrial lobes with short, separate, but adjacent pedicels, each bearing strong bristle; surstylus expanded distally, longitudinally striated, and divided into 3 arms; dorsal surstylar arm narrow; central surstylar arm distally curved; ventral surstylar arm bearing digitiform seta and other short setae as figured; cercus relatively short, with apical blade-like seta and distinctive ventral pedunculate expanded seta on peduncule.

Female: unknown.

Remarks. *Medetera borneensis* has an elongate body form and reduced anal angle, characteristic of the *gracilis* group. However, *M. borneensis* is the least derived of the *gracilis* group, without silvery pruinose body patches and prolonged legs (i.e., It_2 longer than It_1 and TII longer than FII), present in the other members of the group. In cercal structure, *M. borneensis* shows some similarities to *M. vivida.*

Medetera sandakanensis n. sp.

Type material. HOLOTYPE ♂, PARATYPES 2♂♂: **Malaysia:** Sabah: Sandakan Bay (SW), Sapagaya Lumber Camp, 2–20 m, 7 Nov 1957, J.L. Gressitt. PARATYPES: 2♂♂, Kedah: Penang, 22–26 Dec 1958, L.W. Quate (BPBM).

Additional material. Females of either *M. sandakanensis* or *M. penangensis* from type localities (see Remarks below): 5♀♀, **Malaysia:** Sabah: Sandakan Bay (SW), Sapagaya Lumber Camp, 2–20 m, 7 Nov 1957; 7♀♀, Kedah: Penang, 22–26 Dec 1958 (BPBM); possible females of these 2 species: ♀, Sabah (SE): Forest Camp, 19 km north of Kalabakan, 16 Nov 1962 (BPBM); ♀, Kalabakan, 10–19 July 1958 (BPBM). **Laos:** ♀, Vientiane Province, Ban Van Eue, 30 Sept 1967 (BPBM). **Philippines:** ♀, Luzon, Los Banos, April 1914 (ZMH); ♀, Camarines Sur, Mt Isarog, 20 km east of Naga, 6 April 1963 (BPBM).

Description: Male: length 2.9–3.1; wing dimensions 2.8 x 0.6.

HEAD: vertex, frons, metallic green with bronze reflections and some grey pruinosity; clypeus dull metallic green-bronze; proboscis and palpi black; antenna brown; arista length about equal to 1 ½ head height.

THORAX: dorsum, pleurae mostly metallic greenbronze with dusting of grey pruinosity; posterior portion of mesoscutum and scutellum brownish in some specimens; setae black; ac short, less than width of ac band.

SILVERY PRUINOSITY: patches of orientated pruinosity which appear matt grey in lateral perpendicular view but bright silvery when viewed from angle of 0–45 degrees either side of median sagittal plane present on following structures (Fig. 11b): anterior forecoxae, ventral to mesoscutal suture just above notopleural suture, large patch just below notopleural suture, tip of meskatepisternum, top of metepimeron, ventrolaterally on abdominal terga 1 and 2, and posteroventrally on tergum 3.

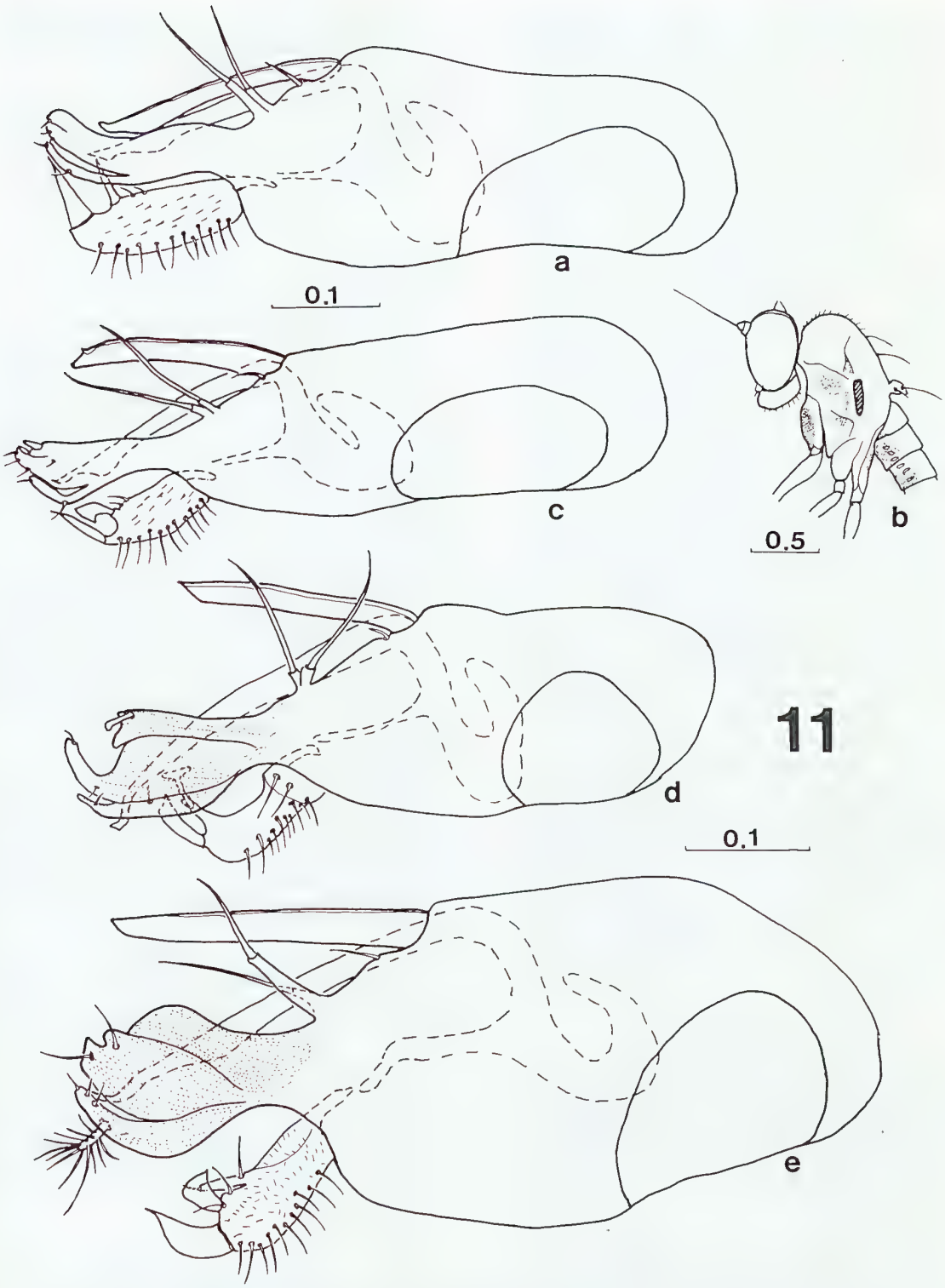

Fig. 11. a–b, *M. sandakanensis,* Sabah; a, hypopygium, left lateral view; b, head, thorax, and anterior abdomen, left lateral view (silvery pruinose patches indicated by stippling). **c,** *M. penangensis,* Penang, Malaysia; hypopygium, left lateral view. **d,** *M. borneensis,* Sabah; hypopygium, left lateral view. **e,** *M. gracilis,* Sumatra; hypopygium, left lateral view.

LEGS: coxa I yellow; coxae II and III dark brown; remainder of legs yellow; I: 2.2; 2.0; 0.7/0.9/0.6/0.3/0.3; It_2 longer than It_1; II: 2.2; 2.5; 1.1/0.9/0.6/0.4/0.3; TII longer than FII; III: 2.2; 2.4; 0.4/1.1/0.6/0.4/0.3.

WING: ovate in shape with reduced anal angle, similar to Fig. 2e; CuAx ratio 0.4; lower calypter yellow with fan of pale setae; haltere yellow.

ABDOMEN: dark metallic green-bronze with short black setulae; hypopygium dark brown with yellow cerci (Fig. 11a); epandrium subrectangular; hypandrium trough-shaped, slightly upturned apically, and almost reaching apex of aedeagus; aedeagus elongate; epandrial seta short, near base of hypandrium; distal epandrial lobe with pedicel much longer than that of basal lobe; surstylus slightly expanded distally, deeply cleft, with narrow dorsal arm and wider ventral arm, and with setae as figured; cercus rather stout, with 2 distinctive ventral setae: stout triangular apical seta and narrower tapering blade-like seta at ⅔.

Female: similar to male, including silvery pruinose patches and shiny metallic blue face.

Remarks. *Medetera sandakanensis* and *M. penangensis* are very closely related species, and males of both species were taken together in mixed series at two rather distant localities in Malaysia: at Sandakan Bay, Sabah, on the north-eastern tip of Borneo, and at Penang, on the western coast of the Malay Peninsula. The two species are identical in all non-genitalic characters, indicating that little character displacement has taken place apart from the hypopygia (all male specimens had to have their genital capsules cleared in order to place them according to the two hypopygial types). The two hypopygial types are constant in their cercal structure and are considered as representing two widespread sympatric sister species. However, the possibility remains that they represent a single species with dimorphic hypopygia.

Females associated with the two species cannot be separated and specimens from localities in the Philippines, Laos, and elsewhere in Sabah may represent them.

Medetera penangensis n. sp.

Type material. HOLOTYPE ♂, PARATYPE ♂: **Malaysia:** Kedah: Penang, 22–26 Dec 1958, L.W. Quate. PARATYPE ♂: Sabah, Sandakan Bay (SW), south of Sapagaya Lumber Camp, 2–20 m, 7 Nov 1957, J.L. Gressitt (all BPBM).

Description. Male: length 2.9–3.1; wing dimensions 2.8 x 0.6; similar in all respects to *M. sandakanensis* except as noted.

ABDOMEN: dark metallic green-bronze with short black setulae; hypopygium dark brown with yellow cerci (Fig. 11c); hypandrium trough-shaped, slightly upturned subapically; epandrial seta short, near base of hypandrium; pedicels of epandrial lobes subequal in length; surstylus slightly expanded distally, deeply cleft, with narrow dorsal arm and wider ventral arm, and with setae as figured; cercus rather stout, with 2 distinctive ventral setae: blade-like apical seta and hatchet-shaped seta at ⅔.

Female: similar to male, including silvery pruinose patches and shining metallic blue face.

Remarks. See Remarks under *M. penangensis*, above.

Medetera gracilis Parent

Medetera gracilis Parent, 1935: 523.
Elongomedetera thoracica Hollis, 1964: 260, n. syn.

Type material. Parent described *M. gracilis* from a single male taken in Sabah, at Bettotan, near Sandakan (BMNH, examined). Hollis described the monotypic genus *Elongomedetera* from Indonesia. He distinguished this genus from *Medetera* by its having an elongate thorax, relatively long legs, and the lack of an anal lobe. However, its hypopygial structure is characteristic of *Medetera* and separate generic status is unwarranted. I have examined together the male holotypes of both *M. gracilis* and *E. thoracica* from Fort de Kock, Sumatra (ZMUA). Despite some variation between the two holotypes, I regard them as conspecific, as will be discussed below.

Additional material. (All BPBM except where noted) **Indonesia:** 1♂, Sumatra, Njuruk Dempu, 1600 m, Aug 1916 (ZMUA). **Malaysia:** Sabah: 1♂, Forest Camp, south-west of Tenom, 19 Dec 1962; 1♂, Tawau, Quoin Hill, Forest Camp, 3–5 km west of Cocoa Res. Stn, 9–20 July 1962. Sarawak: 1♂, 1♀, Kapit Dist., Merirai V., 30–300 m, secondary forest, 1–6 Aug 1958; 1♀, Sadong Kampong, Tapuh, 300–440 m, 10 July 1958. West Malaysia: 1♂, Cameron Highlands, Mt Brichang, 2–7 Jan 1959.

Description. Male: length 2.4–3.2; wing dimensions 2.2–3.0 x 0.6–0.8.

HEAD: vertex, frons, metallic blue-green with some grey pruinosity; clypeus metallic green-bronze with some grey pruinosity; palpi black; proboscis black, massive; antenna dark brown; arista length about equal to 1½ head height.

THORAX: elongate, more than twice as long as wide; dorsum mostly metallic green-bronze anteriorly with dusting of grey pruinosity; posterior mesoscutum and scutellum brownish in some specimens; pleura brownish; setae black; ac biserate, very short and reduced.

SILVERY PRUINOSITY: patches of orientated pruinosity, which appear matt grey in lateral perpendicular view but bright silvery when viewed from angle of 0–45 degrees either side of median sagittal plane, have a distribution similar to *M. sandakanensis* (Fig. 11b).

LEGS: legs elongate; coxa I yellow; coxae II and III yellowish to brown; remainder of legs yellow; leg setae yellowish; I: 2.8; 2.6; 0.9/1.5/1.1/0.4/0.5; II: 3.5; 4.3; 1.5/1.8/1.1/0.5/0.4; TII longer than FII; III: 3.7; 4.3; 0.7/2.2/1.1/0.8/0.5; t_2 distinctly longer than t_1 on all legs.

WING: ovate in shape with greatly reduced anal

angle (Fig. 2e); M gradually approaching R_{4+5} to apex; CuAx ratio 0.4–1.0 (see Remarks below); lower calypter yellow with fan of pale setae; haltere yellow.

ABDOMEN: dark metallic green-bronze with short black setulae; hypopygium dark brown with yellow cerci (Fig. 11e); epandrium rounded subrectangular; hypandrium trough-shaped and not reaching apex of aedeagus; aedeagus elongate, apically upturned; epandrial seta near base of hypandrium; distal epandrial lobe with pedicel much longer than that of basal lobe; surstylus expanded distally and clavate, longitudinally striated, and divided into 3 arms; dorsal surstylar arm bears distinctive stout branched seta; cercus with broad apical blade-like seta, subtended ventrally by smaller blade-like seta and digitiform cuticular projection.

Female: similar to male, including silvery pruinose patches and shiny metallic blue face.

Remarks. *Medetera gracilis* is known from Malaya, Borneo and Sumatra. It is a distinctive species with elongate body and legs, and wings with a reduced anal angle (see Fig. 30 in Hollis, 1964, for habitus), and is the most derived member of the *gracilis* species group. The hypopygium of all male specimens has a distinctive stout branched modified seta on the dorsal surstylar arm.

The holotype of *E. thoracica* has biserial ac, not uniserial as mentioned in Hollis' description. Since the ac are highly reduced, and in some cases absent or not clearly visibe, it might appear that they are uniserial. However, in anterior view, the visible ac are seen to fall into 2 rows.

Some notable variation is evident among nongenitalic characters, especially body and wing length and CuAx ratio. As noted above, male body length ranges from 2.4–3.2, and correspondingly, wing length ranges from 2.2–3.0. This is a fairly large range of variance for *Medetera.* Of the 7 males examined, 6 had a wing length between 2.7 and 3.0, and only one small male from the Kapit District, Sarawak, had a wing length of 2.2. The CuAx ratio range of 0.4–1.0 seems to vary according to wing length, with the small Sarawak male having a ratio of 0.4, while the largest specimen, the *M. gracilis* holotype, has a ratio of 1.0. The other specimens have CuAx ratios of 0.6–0.7.

The distinctive silvery pruinose patches are not always evident on specimens, especially if they appear somewhat teneral with the thorax mostly brownish. However, differentially contrasting pruinosity, even on teneral specimens indicate the presence of these patches.

The *flaviscutellum* Group

The *flaviscutellum* group is characterized by the following features: antennal scape and pedicel yellowish; arista usually long, length 1½ to 2 times head height; scutellum and posterior mesoscutal slope usually yellowbrown; anterior ac short, less than width of ac band, posterior ac just longer than width of ac band; two strong dc bordering mesonotal depression, with the anterior dc much shorter and decreasing anteriorly; abdominal segment 7 somewhat elongated, distinctly longer than segment 6 and with strong development of both tergum and sternum; surstylus usually with membranous attachment to epandrium, although fused in some species; surstyli broad, massive, often with cuticular striae; epandrial lobes usually positioned distad, near join of epandrium and surstylus; aedeagus not internally recurved; cercus upcurved apically, and with ventral projections.

Although the *flaviscutellum* group is not defined by any strong autapomorphy, I believe it forms a monophyletc assemblage based on similarity of hypopygial structure. Most members of group display a yellowish scutellum and posterior mesonotal slope, which grades into metallic green colour anteriorly (see Morphological Note 6).

Male secondary sexual characters on some species include distinctive setation on the femora, and a flattening of the male foretarsus(*M.killertonensis*).

This group is found principally in Australasia although *M. philippinensis* is described from the Philippines. Of the remaining species, *M. killertonensis* and *M. flaviscutellum* are from New Guinea, while *M. dorrigensis, M. uda, M. athertonensis, M. bunyensis* and *M. gingra* are from the forests of eastern Australia.

Medetera flaviscutellum n. sp.

Type material. HOLOTYPE ♂: **Papua New Guinea:** Karimui, south of Goroka, 1000 m, 3 June 1961, J. L. & M. Gressitt (BPBM). PARATYPE: ♂, Woitape, Wharton Range, 20 Oct 1963 (AMS).

Description. Male: length 2.0–2.1; wing dimensions 2.0 x 0.7.

HEAD: vertex, frons, face, clypeus metallic green with brown pruinosity; proboscis brown, massive.

THORAX: anterior mesonotum and pleura dark metallic green with dusting of grey-brown pruinosity; posterior mesoscutal slope yellow; scutellar base greenish, remainder yellow; (in the specimen from Woitape, most of the dorsum is redyellow, and only area anterior to mesoscutal depression is dark green); setae black; ac short, posterior pairs only about as long as width of ac band; 2 strong dc bordering mesoscutal depression, anterior dc as short setulae; median scutellars strong, laterals about ½ length of medians.

LEGS: coxa I yellow, coxae II, III yellow to infuscated; remainder of legs entirely yellow; relative podomere lengths as: I: 2.4; 2.1; 0.6/0.4/0.3/0.2/0.2; II: 2.6; 2.4; 1.1/0.6/0.4/0.3/0.3; III: 2.8; 3.0; 0.5/1.1/0.5/0.3/0.3.

WING: M gradually approaches R_{4+5} (Fig. 2g);

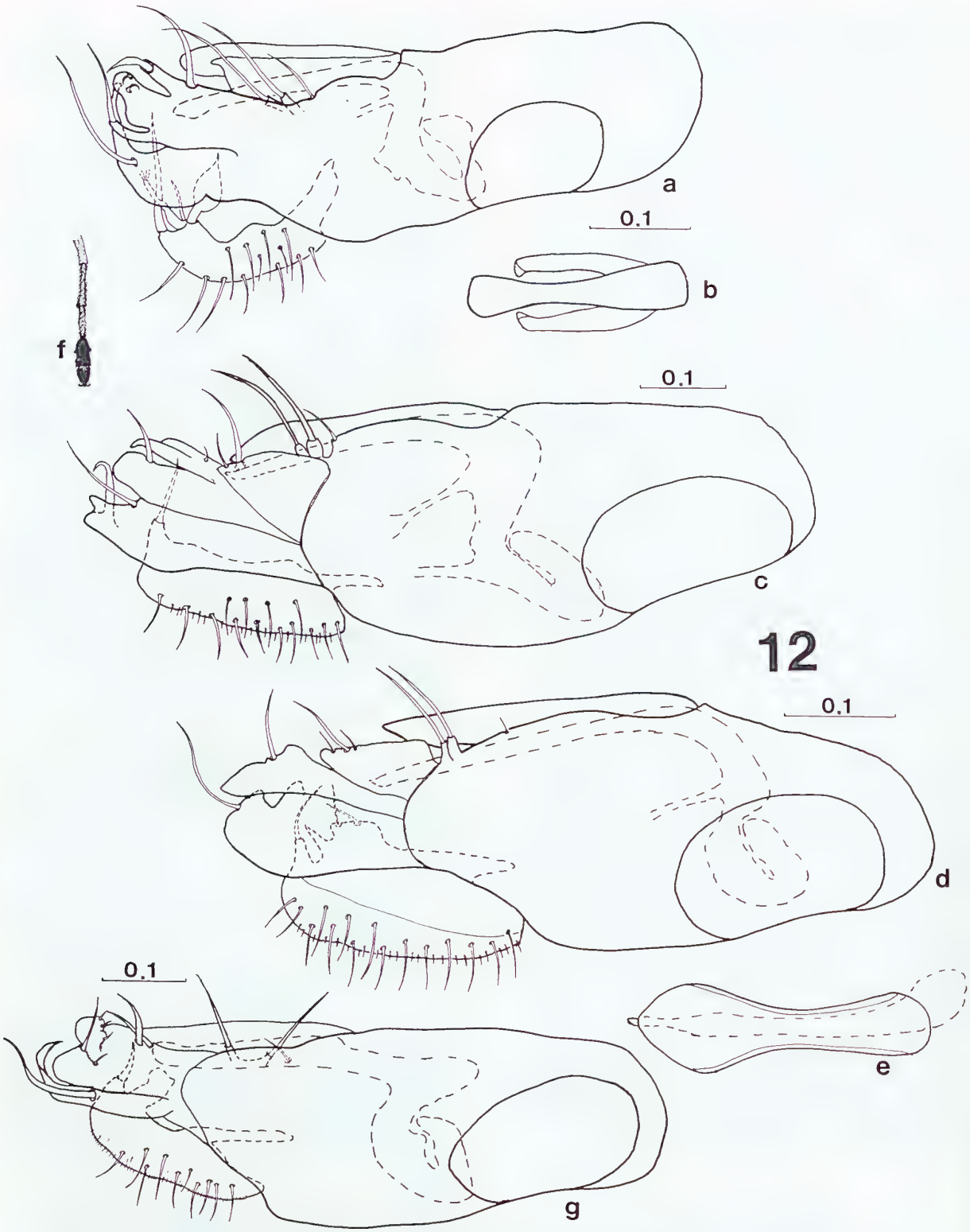

Fig. 12. a–b, *M. athertonensis,* Atherton, Queensland; a, hypopygium, left lateral view; b, hypandrium, ventral view. **c,** *M. flaviscutellum,* Goroka, Papua New Guinea; hypopygium, left lateral view. **d–f,** *M. killertonensis,* Cape Killerton, Papua New Guinea; d, hypopygium, left lateral view; e, hypandrium and aedeagus, ventral view; f, male left tarsus I, anterior view. **g,** *M. philippinensis,* Luzon; hypopygium, left lateral view.

CuAx ratio 0.4; lower calypter yellow with distinct brown rim and fan of pale setae; haltere yellow.

ABDOMEN: black with metallic green reflections and with short black setulae; hypopygium dark brown with yellowish cerci (Fig. 12c); epandrial seta well developed and positioned near epandrial lobes; surstylus with cuticular striae; dorsal surstylar arm with large subapical median cuticular hook-like projection; ventral surstylar arm with basal subtriangular section bearing strong ventral seta; cercus subrectangular in lateral view with strong apicoventral seta.

Female: unknown.

Remarks. *Medetera flaviscutellum* and *M. killertonensis* have a similar hypopygial structure and are probably closely related.

Medetera killertonensis n. sp.

Type material. HOLOTYPE ♂: **Papua New Guinea:** Cape Killerton, malaise trap, 0–5 m, 6–13 May 1965, W. A. Steffan (BPBM).

Description. Male: length 1.8; wing dimensions 1.8 x 0.6; similar to *M. flaviscutellum* except as noted.

THORAX: anterior mesonotum and pleura metallic green with bronze reflections and covered with grey pruinosity; posterior mesonotum and scutellum yellowish; major setae black, shorter setae brownish; chaetotaxy similar to *M. flaviscutellum* except lateral scutellars reduced to short hairs, less than ¼ length of medians.

LEGS: coxae brown, remainder of legs yellow except where noted; relative podomere ratios similar to *M. flaviscutellum;* It_{3-5} flattened, black, forming an ovate 'flag', in sharp contrast to pale basal tarsomeres (MSSC)(Fig. 12f); FIII with 4 strong pale anterior setae on distal half.

WING: CuAx ratio 0.5; lower calypter and haltere entirely yellow.

ABDOMEN: black with metallic green reflections; hypopygium dark brown with yellowish cerci (Fig. 12d); hypandrium in ventral view expanded subapically (Fig. 12e); aedeagus simple, tapering; epandrial seta short, positioned basad of epandrial lobes; epandrial lobes adjacent to suture between surstylus and epandrium; surstylus with cuticular striae; dorsal surstylar arm with long apical seta; ventral surstylar arm with basal subtriangular section and with setae as figured; cercus massive, stout, and with ventral projections and setae as figured, and with strong apicoventral seta, similar to *M. flaviscutellum.*

Female: unknown.

Remarks. The flattened leg I tarsomeres 3–5 in *M. killertonensis* represents an independent development of this male secondary sexual character in *Medetera.* Flattened male foretarsi, usually involving only tarsomeres 2 and 3, are common in the *aberrans* group (q.v.).

Medetera philippinensis n. sp.

Type material. HOLOTYPE ♂: **Philippines:** Luzon, Dalton Pass, Nueva Vizcaya, 9–10 April 1968, collector unknown (BPBM).

Description. Male: length 3.0; wing dimensions 2.9 x 0.8.

HEAD: vertex, frons, face, clypeus metallic green with some silvery pruinosity; proboscis brown; arista about as long as head height.

THORAX: anterior mesonotum metallic green with bronze reflections; posterior mesoscutum, scutellum and metapostonum yellowish; thoracic setae pale; major thoracic setae missing on specimen but apparently strong median and lateral scutellars present.

LEGS: coxae yellow, although coxae II and III infuscated basally; remainder of legs yellow; relative podomere ratios as: I: 1.7; 1.4; 0.6/0.5/0.4/0.3/0.3; II: 2.0; 2.1; 0.9/0.6/0.4/0.3/0.2; III: 2.1; 2.5; 0.5/1.0/0.4/0.3/0.3.

WING: venation similar to *M. flaviscutellum;* CuAx ratio 0.4; lower calypter yellow with fan of pale setae; haltere yellow.

ABDOMEN: dark metallic green with bronze reflections and covered with short yellowish setulae; hypopygium dark brown with yellowish cerci (Fig. 12g); epandrium elongate; hypandrium and aedeagus simple; epandrial lobes diverging; surstylus with membranous connection to epandrium; dorsal surstylar arm becoming ribbon-like distally and curving mediad, and bearing strong external seta; ventral surstylar arm lobate, with 2 strong ventral setae and other setae as figured; cercus massive, bearing strong apicoventral seta, subtended ventrally by strong lobate projection.

Female: unknown.

Medetera dorrigensis n. sp.

Type material. HOLOTYPE ♂ (ANIC), PARATYPES 11♂♂, 10♀♀ (ANIC, AMS): **Australia:** New South Wales, Dorrigo National Park, 24 Oct 1980, D. J. Bickel.

Description. Male: length 2.4; wing dimensisons 2.3 x 0.9.

HEAD: vertex, frons, face, clypeus metallic green with bronze reflections, and with dusting of grey pruinosity; proboscis black.

THORAX: dorsum metallic bronze-green with dusting of grey-brown pruinosity; pleura with dense grey pruinosity; scutellum varies from yellowish to greenbrown with only yellowish rim in some specimens; ac short, but posterior pair, just anterior to mesonotal depression is particularly strong, longer than width of ac band; median scutellars strong, the laterals as weak hairs, less than ¼ length of medians.

LEGS: coxae brown with metallic green reflections; basal half of femora yellow to brown; remainder of legs yellow; relative podomere ratios as: I: 2.1; 1.8;

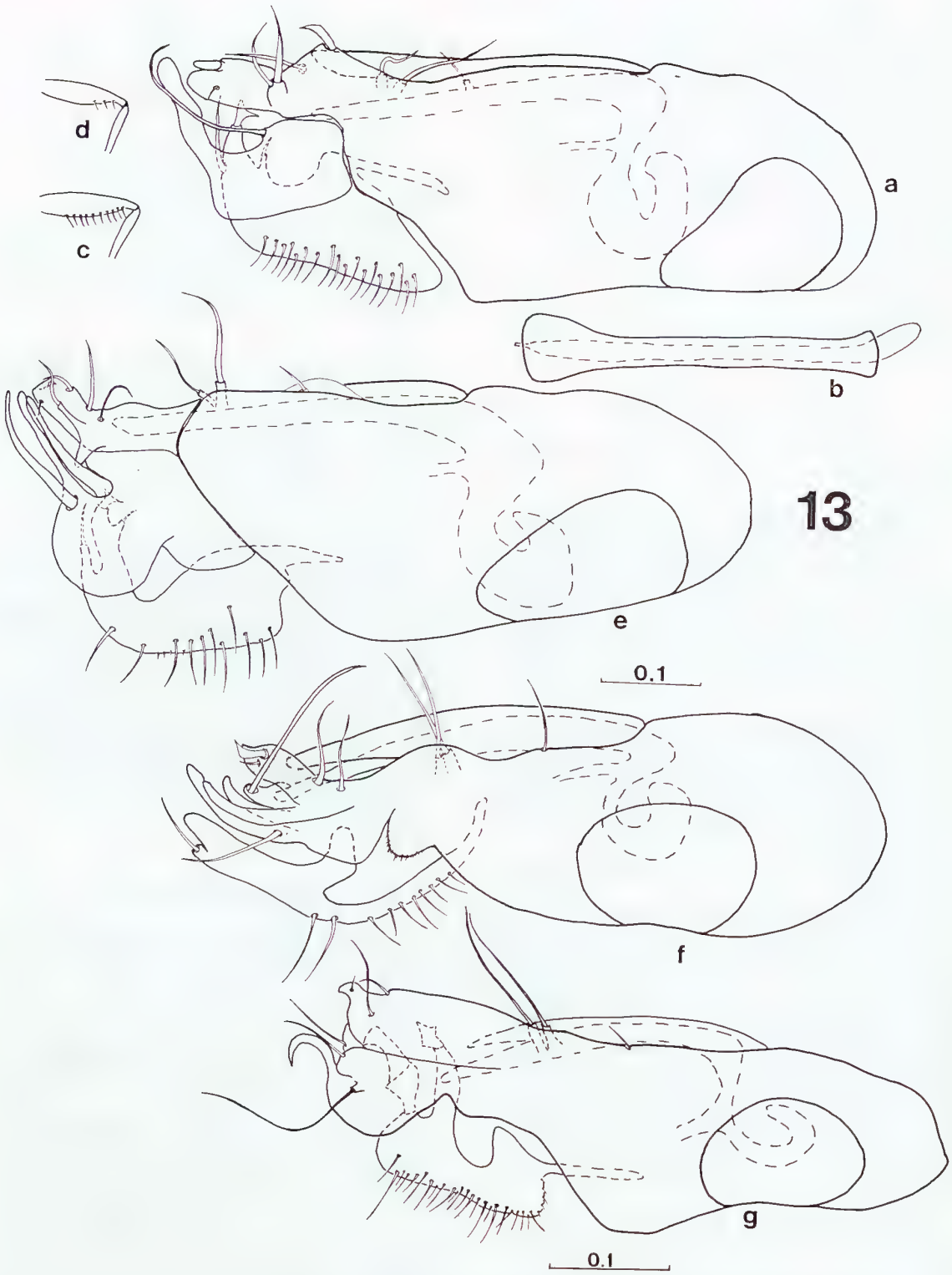

Fig. 13. a–d, *M. dorrigensis,* Dorrigo, New South Wales; a, hypopygium, left lateral view; b, hypandrium and aedeagus, ventral view; c, male left femur II, anterior view; d, female left femur III, anterior view. **e,** *M. uda,* Dorrigo, New South Wales; hypopygium, left lateral view. **f,** *M. gingra,* Blue Mountains, New South Wales; hypopygium, left lateral view. **g,** *M. bunyensis,* Bunya Mountains, Queensland; hypopygium, left lateral view.

0.7/0.5/0.4/0.3/0.3; FI ventrally with 6–7 long pale setae (MSSC); II: 2.1; 2.0; 0.9/0.5/0.3/0.2/0.2; FII ventrally on basal half with row of 5–6 pale setae, on distal half continuing as row of 5–6 dark spine-like setae (MSSC)(Fig. 13c); III: 2.2; 2.5; 0.5/0.9/0.4/0.2/0.3; FIII anteroventrally along entire length with row of 8–10 long pale setae (MSSC).

WING: similar to Fig. 2g; CuAx ratio 0.4; lower calypter yellow with dark brown rim and with fan of pale setae; haltere yellow.

ABDOMEN: black with metallic green reflections and with short black setulae; hypopygium black with brownish cerci (Fig. 13a); epandrium with transverse cuticular striae; hypandrium elongate, subrectangular, and expanded apically in ventral view (Fig. 13b); aedeagus tapering, simple; epandrial seta arising internally in lateral view, and with short peduncular base; bristle of basal epandrial lobe longer than that of distal lobe; surstylus massive; dorsal surstylar arm with apical lobate projection and bearing long curved external seta near base; ventral surstylar arm with bladelike setal projection on triangular mound and with other major setae as figured; cercus distally upcurved and with strong outer seta, apical anvil-shaped seta, and inner short pedunculate seta as figured.

Female: similar to male except as noted: FI, FII lacking distinctive ventral setae; FIII with 2-3 long pale anteroventral setae in distal ¼ (Fig. 13d).

Remarks. Specimens of *M. dorrigensis* and *M. uda* were taken together in a mixed series of 38 individuals. Both species were collected in the early morning off trunks of pencil cedar, *Polyscias elegans* (Araliaceae) at the 'Glades Picnic Ground', Dorrigo National Park. The surrounding vegetation is subtropical rainforest. These two sympatric species are virtually identical except for details of the male femoral setation and genitalia, and they are probably sister species. The development of distinctive femoral setation is also evident in female *M. dorrigensis,* such that females have three distinctive FIII setae, which are lacking in female *M. uda.*

Medetera uda n. sp.

Type material. HOLOTYPE ♂ (ANIC), PARATYPES 4♂♂, 11♀♀ (ANIC, AMS): **Australia:** New South Wales, Dorrigo National Park, 760 m, 24 Oct 1980, D. J. Bickel.

Additional material. New South Wales: 1♂, Mt Warning National Park, rainforest, on trunk *Archontophoenix cunninghamiana* (Palmae), 24 Nov 1985 (AMS). Queensland: 1♂, Lamington National Park, O'Reilly's, rainforest, malaise trap, 3 Feb to 2 March 1980 (QDPI).

Description. Male: this species is similar in all respects to *M. dorrigensis,* except as noted.

LEGS: femora I and III without long ventral setae; femur II only with scattered weak ventral setae basally, lacking dark anteroventral setae on distal half.

ABDOMEN: hypopygium black with brown cerci (Fig. 13e); epandrium with cuticular striae; epandrial seta short; basal epandrial lobe much larger than distal lobe; surstylus with membranous attachment to epandrium; dorsobasally, surstylus weakly sclerotized near junction with epandrium; dorsal surstylar arm massive with large dorsoapical development and with large stout projecting seta and with lateral triangular projection as figured; ventral surstylar arm with setae and cuticular projections as figured; cercus distally upcurved with outer seta on cuticular pedicel, apical anvil-shaped seta, and short inner pedunculate seta.

Female: similar to female *M. dorrigensis* except lacking long pale anteroventral setae on FIII.

Remarks. *Medetera uda* is found in subtropical rainforest in north-eastern New South Wales and southeastern Queensland. It has been collected off the trunks of smooth barked trees, off pencil cedar at Dorrigo and off bangalow palm at Mt Warning. *Medetera uda* possibly represents an ancestral type from which the more derived *M. dorrigensis* (with distinctive MSSC leg setation) could have arisen.

Medetera athertonensis n. sp.

Type material. HOLOTYPE ♂: **Australia:** Queensland, Wongabel State Forest near Atherton, 17°20′S 145°31′E, malaise trap, 19 Nov 1981, D. H. Colless (ANIC).

Description. Male: length 2.0; wing dimensions 1.8 x 0.8; similar to *M. dorrigensis* except as noted.

LEGS: podomere ratios similar to *M. dorrigensis;* lacking distinctive setation on F II and III.

WING: CuAx ratio 0.3.

ABDOMEN: hypopygium dark brown with yellowish cerci (Fig. 12a); hypandrium with pair of lateral winglike processes arising basad, and aedeagus apically clavate in ventral view (Fig. 12b); epandrial lobes each with collar-like pedicel; surstylus broad and divided into dorsal and ventral arms; dorsal surstylar arm narrowed and ventrally curved distad, and with a strong lateral seta; ventral surstylar arm with strong setae and cuticular projections as figured; cercus upcurved distally, with distinctive apical projections, including an elongate outer seta and large leaf-shaped inner seta.

Female: unknown.

Medetera gingra n. sp.

Type material. HOLOTYPE ♂: **Australia:** New South Wales, Blue Mtns, Kanangra-Boyd National Park, junction Kowmung River and Gingra Creek, 12 Oct 1980, D. J. Bickel (ANIC). PARATYPES: 1♂, 2♀♀, 30 km north of Taree, Pacific Hwy, on *Eucalyptus* sp., 23 Nov 1985 (AMS); 1♂, 1♀, Queensland: Bunya Mountains National Park, Horse Gully Creek, on *E. punctata,* 6 Dec 1985 (AMS).

Description. Male: length 2.6; wing dimensions 2.3 x 0.8.

HEAD: vertex, frons, face, clypeus black with dusting of grey pruinosity; proboscis dark brown-black; arista about as long as head height.

THORAX: dorsum metallic green-bronze with some grey pruinosity; pleura with dense grey pruinosity; scutellum entirely dark, without yellow-brown colouration; setae yellowish; lateral scutellars ⅔ length of medians.

LEGS: coxae dark brown, becoming yellowish distally; legs yellowish although femora brownish dorsally and basally; relative podomere ratios as: I: 3.2; 2.7; 1.1/0.8/0.6/0.4/0.4; II: 3.4; 3.1; 1.9/0.9/0.5/0.4/0.4; III: 2.9; 3.6; 0.8/1.7/0.8/0.4/0.3.

WING: elongate; M gradually approaches R_{4+5}; CuAx ratio 0.3; lower calypter yellow with fan of pale setae; haltere yellow.

ABDOMEN: dark metallic green-bronze with short yellowish setulae; hypopygium dark brown with yellowish cerci (Fig. 13f); epandrium elongate with cerci held between surstyli at rest; hypandrium and aedeagus simple; epandrial seta strong, positioned midway between epandrial lobes and base of hypandrium; junction of epandrium and surstylus fused but marked dorsally by deep cleft; dorsal surstylar arm elongate, tapering with strong lateral seta; ventral surstylar arm with striated lobe bearing subapical setal flag and subtended by strong seta projecting ventrad; other surstylar lobes and setae as figured; cercus narrow basally, with midventral lobe marking beginning of wider distal half which bears thin dorsoapical seta.

Female: similar to male.

Remarks. All specimens of *Medetera gingra* were collected off the trunks of *Eucalyptus* spp. in dry and wet sclerophyll forest from the Blue Mountains, New South Wales, to southern Queensland. Neither this species nor *M. bunyensis* has the yellowish posterior mesonotum and scutellum found in other members of the *flaviscutellum* group.

Medetera bunyensis n. sp.

Type material. HOLOTYPE ♂, PARATYPE ♂: **Australia:** Queensland: Bunya Mountains National Park, Horse Gully Creek, on *Eucalyptus punctata,* 6 Dec 1985, D. J. Bickel (AMS).

Description. Male: length 2.4; wing dimensions 1.9 x 0.8; similar to *M. gingra* except as noted.

THORAX: also with metallic green scutelum and yellowish setae.

ABDOMEN: dark metallic green-bronze with short yellowish setulae; hypopygium dark brown with yellowish cerci (Fig. 13g); epandrium subrectangular; hypandrium and aedeagus simple; epandrial seta relatively short, positioned midway between epandrial lobes and base of hypandrium; epandrial lobes strong; epandrium and surstylus fused; dorsal surstylar arm with distinctive strong cuticular hook and elongate lateral seta; ventral surstylar arm with striated lobe bearing setae as figured; cercus blunt apically, with midventral excavation and with with 2 strong ventral projections as figured.

Female: unknown.

Remarks. Both specimens of *Medetera bunyensis* were collected off the smooth trunks of *Eucalyptus punctata* in the Bunya Mountains, Queensland. This species is closely related to *M. gingra,* and they occur sympatrically, having been collected together off the same trees.

The *salomonis* Group

The *salomonis* group is characterized by the following: antennal colour various, either all black or with scape and pedicel yellow; thoracic setae black; either 5–6 dc present, or with 2 strong dc bordering mesoscutal depression and only short setulae present anteriorly; males with pale subapical dosal seta on TIII (MSSC) (group autapomorphy); males sometimes with distinctive ventral setae on femora, or with orientated silvery pruinosity (MSSC); in *M. femoralis,* both male and female have orientated silvery pruinoisity; wing vein M often either straight or bowed posteriorly (Figs 2a–c) (group autapomorphy); cercus secondarily segemented, with distal section of cercus articulated with basal section (strong group autapomorphy); tendency for distal section of cercus to become enlarged and expanded, sometimes with corresponding decrease in strength of surstylus (e.g., Fig. 15c).

The *salomonis* group has radiated primarily in Australasia but it also has spread into the Oriental region. *Medetera olivacea,* with a distribution from south-eastern Asia to New Guinea, has a posteriorly bowed vein M. Although its cercus is not articulated, the distal portion is distinctly demarcated, and this condition might be regarded as ancestral for the group. The *salomonis* group s.s. with an articulated distal section of the cercus might be divided into 2 assemblages:

1. *Medetera nigrohalterata, M. mooneyensis* and *M. austrofemoralis,* all from Australia, have the antenna black and 2 strong dc bordering the mesoscutal depression.

2. *Medetera salomonis* (widespread Australasia, Philippines), *M. femoralis* (New Guinea), *M. pseudofemoralis* (Melanesia, Queensland) and *M. malayensis* (Malaya) have the scape and pedicel yellow and 4–6 strong dc, decreasing in size anteriorly.

The secondary segmentation and articulation of the cercus is an unusual character, possibly unique in the Diptera Brachycera.

Medetera olivacea de Meijere

Medeterus olivaceus de Meijere, 1916: 260.

Type material. De Meijere described *M. olivaceus* from

4♀♀ syntypes taken at Batavia, Java. I have designated a ♀, bearing the label "Batavia/ iv 1908/ E. Jacobson" as LECTOTYPE (ZMUA, examined).

Additional material. (All BPBM except where noted) **Indonesia:** Sumatra, Fort de Kock, Oct 1913 (ZMUA). Irian Jaya: Nabire, 5–50 m, 25 Aug to 2 Sept 1962; HollandiaBinnen, 100 m, 31 Oct 1958; Bodem-Sarmi Aarea, 10 July 1959; Waris, south of Hollandia, 450–500 m, 8–15 Aug 1959; Japen Island, south-south-east Sumberbaba, Dawai River, 2 Nov 1962. **Malaysia:** Sabah: Paring, near Ranau, 23 Jan 1958; Tawau Residency, Kalabakan River, primary forest, 9–18 Nov 1958; Tawau, Quoin Hill, 3–7 July 1962; Sandakan Bay, Sapagaya Lumber Camp, 8 Nov 1957; Kalakakan, primary forest, 30 Oct 1962. **Papua New Guinea:** Wau, Morbe District, 1150–1200 m, Jan, March, April, Aug, Nov, 1962, 1965; Sepik-Maprik, 160 m, 27 Aug 1957. **Philippines:** Camarines Sur, Mt Isarog, 750–800 m, 24 April 1963. (10♂♂, 20♀♀ specimens examined).

Description. Male: length 2.5–2.6; wing dimensions 2.4 x 0.8.

HEAD: vertex, frons metallic green with bronze reflections and with grey pruinosity; face, clypeus metallic blue-green with grey pruinosity; proboscis black; antenna black; arista about as long as head height.

THORAX: dorsum metallic green with bronze reflections; pleura covered with dense grey pruinosity; ac about as long as width of ac band; 5–6 dc present, with 2 strong dc bordering mesonotal depression and 3–4 shorter dc anteriorly, and with short setulae anteriormost; lateral scutellars about ¼ length of medians.

LEGS: coxae and remainder of legs entirely black; relative podomere ratios as: I: 2.3; 2.0; 1.0/1.0/0.7/0.4/0.3; II: 2.6; 2.4; 1.6/1.0/0.7/0.3/0.3; III: 2.5; 2.9; 0.7/1.5/0.8/0.4/0.3.

WING: venation similar to Fig. 2b; CuAx ratio 0.7; lower calypter and haltere yellow.

ABDOMEN: dark metallic green-bronze with short black setulae; hypopygium dark brown with yellowish cerci (Fig. 14a); epandrium elongate; hypandrium and aedeagus elongate, tapering; epandrial seta strong, arising from short pedicel, and positioned closer to epandrial lobes than base of hypandrium; epandrial lobes each bearing strong bristle and long collar-like base; surstylus with weak membranous attachment to epandrium; surstylus divided into 3 arms, ventral arm with 2 strong ventrally projecting setae, middle arm clavate and weakly sclerotized, dorsal arm elongate; cercus with distinct adjoining but not articulated basal and distal sectors; basal sector with ventral seta and distal sector with 2 strong blade-like setae.

Female: similar to male but lacks MSSC..

Remarks. *Medetera olivacea* is distributed from the Philippines and Borneo through Indonesia to New Guinea (Fig. 23). In some respects, this species could be regarded as ancestral to the remaining *salomonis* group: the cercus is demarcated into distinct basal and distal sections, the basal section bearing a strong ventral seta and the distal section with 2 blade-like seta. Such a demarcation might be ancestral to the articulated cercus of the *salomonis* group as seen in *M. mooneyensis.*

Medetera mooneyensis n. sp.

Type material. HOLOTYPE ♂: **Australia:** New South Wales, Mooney Mooney Creek near Gosford, wet sclerophyll forest, 1 Jan 1975, D. K. McAlpine (AMS). PARATYPES: 1♂, same data but 29 Nov 1975; 4♀♀, same data but 3 Dec 1984; 2♂♂, Mosman, on *Angophora costata,* 2 Dec 1984 (AMS, ANIC).

Description. Male: length 1.8; wing dimensions 1.8 x 0.7.

HEAD: vertex, frons, face black with brown pruinosity; clypeus shiny black; proboscis and antenna black; arista about as long as head height.

THORAX: dark metallic green with bronze reflections; bronze vittae over ac band and laterally over dc row; ac increasing in length posteriorly, the posteriormost about as long as width of ac band; 2 strong dc bordering mesonotal depression, anterior dc as short setulae; lateral scutellars about ⅓ length of medians.

LEGS: coxae, legs dark brown to black; relative podomere ratios as I: 1.7; 1.5; 0.6/0.4/0.3/0.2/0.1; II: 1.8; 1.7; 0.9/0.6/0.4/0.2/0.2; FII with row of black spine-like setae along entire ventral margin (MSSC); III: 1.9; 2.2; 0.5/1.0/0.5/0.3/0.2; TIII with strong pale dorsal at ⅘, not subapically.

WING: M almost straight, only slightly bowed anteriorly; CuAx ratio 0.5; lower calypter entirely yellow with fan of yellow setae; haltere pale yellow.

ABDOMEN: black with metallic green and bronze reflections, and with short black setulae; hypopygium dark brown with yellowish cerci (Fig. 14b); hypandrium and aedeagus simple; epandrial seta short, positioned midway between epandrial lobes and base of hypandrium; epandrial lobes positioned distally, distalmost lobe almost twice as long as proximal lobe; surstylus with membranous attachment to epandrium; surstylus with broad base and strong ventral hump, and continuing distally as single fused arm; surstylus with distinctive costate seta ventrally, median seta bearing projection, and short setae as figured; cercus divided into distinct setose basal section and articulated distal cap-like section; distal cercus with strong striated curved dorsoapical seta and ventroapical cuticular projection with basal and distal setae as figured.

Female: similar to male but lacks MSSC.

Remarks. *Medetera mooneyensis* is known only from the Sydney district and is relatively small in comparison with other members of the group. This species represents the most plesiomorphic condition within the *salomonis* group regarding the development of a secondarily divided and articulated

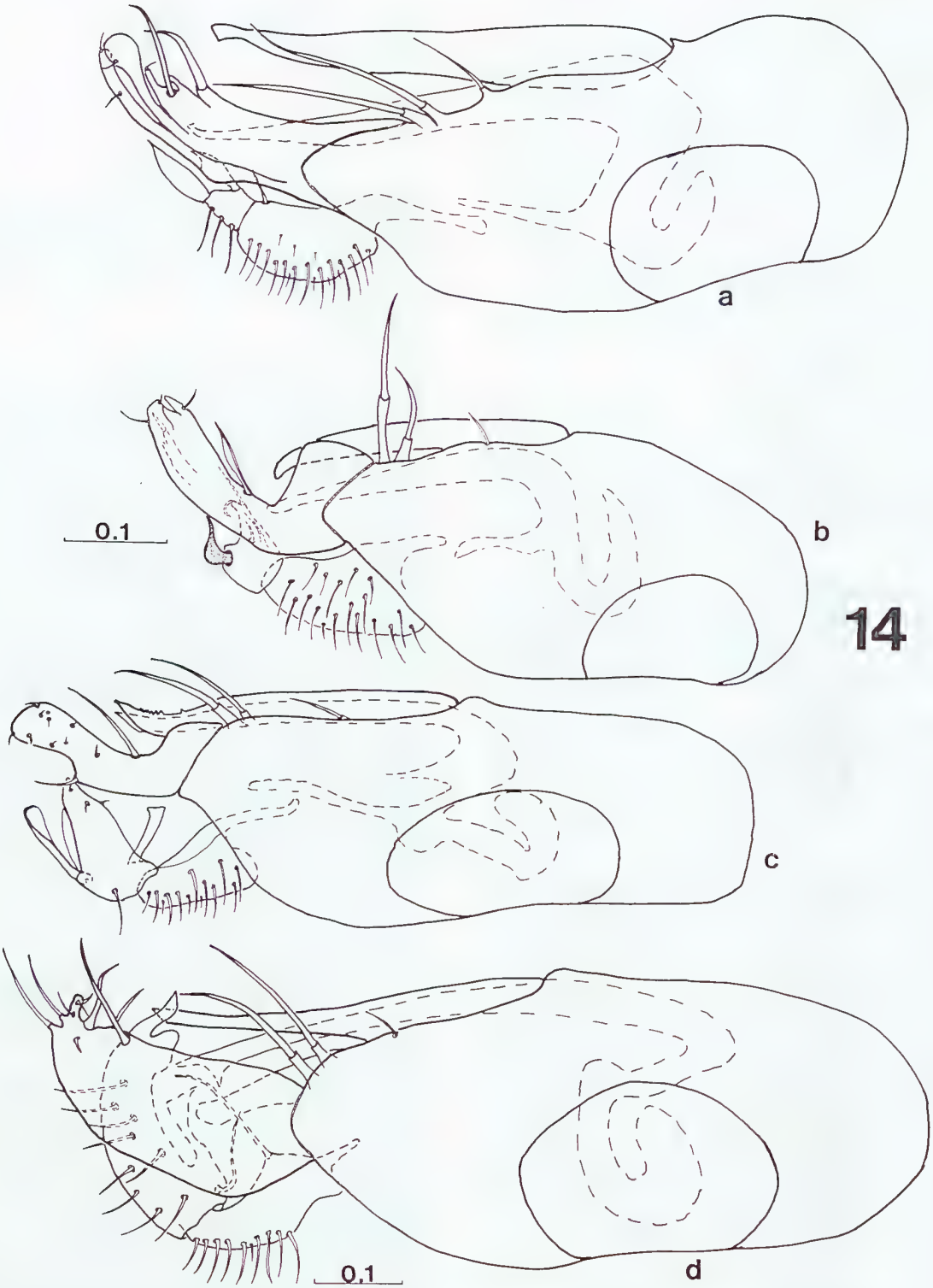

Fig. 14. a, *M. olivacea*, Selangor, Malaysia; left lateral view. b, *M. mooneyensis*, Gosford, New South Wales; hypopygium, left lateral view. c, *M. nigrohalterata*, Broken Bay, New South Wales; hypopygium, left lateral view. d, *M. malayensis*, Kulala Lumpur, Malaysia; hypopygium, left lateral view.

cercus. Here the distal cercus is cap-like and not as expanded or freely articulated as in other members of the *salomonis* group. The venation is plesiomorphic with respect to the rest of the *salomonis* group in that M is slightly bowed anteriorly.

Medetera nigrohalterata Parent

Medetera nigrohalterata Parent, 1932a: 175.

Type material. HOLOTYPE ♀: **Australia:** Australian Capital Territory, Brindabella Rd, bred from *Xanthorrhoea* sp., A. M. Wade (ANIC, examined).

Additional material. Australia: Australian Capital Territory: Mt McDonald, north of Cotter Dam. New South Wales: Broken Bay; Batemans Bay; Narooma, on trunks *Eucalyptus maculata;* Dromedary Ck, near Central Tilba, on trunks *E. maculata;* Meadowbrook; Washpool National Park, near Baryugil, on trunks *Eucalyptus* sp.; Mosman, on trunks *Angophora costata* and *Ficus macrophylla;* Ku-ring-gai Chase National Park; Royal National Park, on trunks *E. haemastoma;* Tinda Creek, Putty Rd, on trunks *Eucalyptus* sp. (collection dates A.C.T. and N.S.W.: Sept to May inclusive). South Australia: Taratap Stn, 36°37′S 139°57′E, 23 Jan 1965. Western Australia: Darling Ranges, John Forrest National Park, 22 Jan 1971. (83 specimens examined: AMS, ANIC, BMNH, SAM).

Description. Male: length 2.1–2.2; wing dimensions 2.2 x 0.8.

HEAD: vertex, frons, face, clypeus black with brown pruinosity; proboscis black; antenna black; arista relatively short, length less than head height.

THORAX: black with metallic green reflections and with brown pruinosity dorsally and grey pruinosity on pleura; ac relatively short, less than width of ac band; 2 strong dc bordering mesonotal depression, anterior dc as short setulae; lateral scutellars about ⅓ length of medians.

LEGS: coxae, legs black, with short pale hairs; relative podomere ratios as: I: 1.9; 1.6; 0.8/0.5/0.3/0.2/0.2; II: 2.3; 1.9; 1.1/0.6/0.4/0.2/0.2; III: 2.2; 2.5; 0.6/1.0/0.6/0.3/0.3; FIII and TIII with short silvery hairs anteriorly.

WING: (Fig. 2c); M with distinctive curvature, slightly flexed just before apex; although M sometimes bowed as in *M. salomonis* (Fig. 2b); CuAx ratio 1.0; lower calypter yellow with distinct brown rim and fan of pale yellow setae; haltere stem and club blackish.

ABDOMEN: black with short black setulae; hypopygium dark brown with yellowish cerci (Fig. 14c); epandrium elongate; hypandrium with subapical denticles on ventral surface; aedeagus elongate, tapering; epandrial seta midway between epandrial lobes and base of hypandrium; pedicel of distal epandrial lobe larger than that of adjacent proximal lobe; surstylus with membranous attachment to epandrium; surstylus fused as single arm, curved with strong ventral seta at base of curvature, short setae distally, and dorsal seta; cercus divided into articulated basal and distal sections; basal section with dorsal setae; distal section of cercus with ventral rectangular projection basally and a clavate distal arm and both can move with respect to expanded midsection; distal section of cercus with strong dorsal seta.

Female: similar to male but lacks MSSC.

Remarks. *Medetera nigrohalterata* is found along the coast and ranges of south-eastern Australia from New South Wales to South Australia, and also in southwestern Australia (Fig. 24). The specimens from the Darling Ranges, Western Australia, have fewer subapical denticles on the hypandrium, otherwise they are identical to specimens from New South Wales and South Australia. The presence of isolated populations of *M. nigrohalterata* in eastern Australia and Western Australia suggests a great age for the species, which must have been widely distributed across southern Australia before increasing post-Miocene aridity split the species into two isolated populations.

Medetera malayensis n. sp.

Type material. HOLOTYPE ♂: **Malaysia:** Kuala Lumpur, Klang Gates, 31 Dec 1958, L. W. Quate (BPBM).

Additional material. 3 probable ♀♀ of this species: **Malaysia:** Pahang, Kuala Tahan, 12–14 Dec 1958. Sabah (SE), Forest Camp, 19 km north of Kalabakan, 60 m, 17 Oct 1962; Sarawak: Gomatong Caves, 22–26 Nov 1958 (BPBM).

Description. Male: length 2.6; wing dimensions 2.5 x 0.9; the holotype is badly greased and rubbed.

HEAD: vertex, frons metallic green with bronze reflections; face and clypeus satiny metallic blue; proboscis black; scape and pedicel yellow; 1st flagellomere dark brown; arista about 1½ as long as head height.

THORAX: dorsum dark metallic green with bronze reflections; ac increasing in length posteriorly, posteriormost as long as width of ac band; 4 strong dc present, decreasing in size anteriorly, and with short setulae anteriormost.

LEGS: coxae, legs black; relative podomere ratios as: I: 2.5; 2.2; 1.4/1.0/0.7/0.4/0.3; II: 3.0; 2.7; 2.0/1.0/0.7/0.3/0.2; III: 3.0; 3.5; 0.8/1.7/1.0/0.4/0.3.

WING: venation similar to *M. salomonis* (Fig. 2b); CuAx ratio 0.7; lower calypter yellow with fan of pale setae; haltere yellow.

ABDOMEN: dark metallic green-bronze with short black setulae; hypopygium dark brown with yellowish cerci (Fig. 14d); hypandrium elongate, simple; aedeagus elongate, slightly recurved within epandrium, and with subapical dorsal triangular projection visible in lateral view; epandrial seta short, positioned midway between epandrial lobes and base of hypandrium; epandrial lobes subequal, each bearing strong bristle; surstylus with membranous attachment to epandrium; cuticular projection present along ventrolateral wall of genital chamber

adjacent to epandrial lobes and base of surstylus; surstylus as single broad arm, with 2 strong ventral bristles and other setae as figured; basal section of cercus with single strong projecting ventral seta and usual short dorsal setae; distal section of cercus curved with apical cuticular projections, and bearing strong ventrobasal curved seta and midventral blade-like projection.

Female: similar to male but lacks MSSC.

Remarks. *Medetera malayensis* is known from the Malay Peninsula and northern Borneo. It is the only wholly Oriental member of the *salomonis* group.

Medetera austrofemoralis n. sp.

Type material. HOLOTYPE ♂, PARATYPES 1♂, 1♀: **Australia:** Queensland, 1.5 km north of Lawgi, 11 May 1955, K. Norris & I. F. B. Common. PARATYPE: ♂, Mt Cook National Park, near Cooktown, 11–12 Oct 1980 (ANIC).

Description. Male: length 2.3; wing dimensions 2.1 x 0.8.

HEAD: vertex, frons and face metallic green and covered with brown pruinosity; clypeus metallic green with bronze reflections; proboscis black; antenna dark brown; arista about as long as head height.

THORAX: dorsum metallic green with bronze reflections covered with dusting of brown pruinosity; pleura covered with dense orientated pruinosity which appears silvery when viewed anteriorly through an arc 45 degrees either side of median saggital plane, and thus not appearing silvery in lateral view (MSSC); setae black; ac increasing in length posteriorly, the posteriormost about as long as width of ac band; 2 strong dc bordering mesonotal depression with anterior dc as short setulae; lateral scutellars about ½ length of medians.

LEGS: coxae, femora, tibiae black; tarsi yellowish but darkened distally; mass of silvery hairs present on anterior surfaces of femora and tibiae II and III, such that underlying dark cuticle is totally obscured, but silvery hairs somewhat wider and denser on TII (MSSC); posterior surfaces of legs black with pale normal vestiture; relative podomere ratios as I: 2.0; 1.8; 0.9/0.5/0.5/0.3/0.3; II: 2.3; 2.0; 1.0/0.5/0.4/0.3/0.2; III: 2.1; 2.4; 0.5/1.1/0.7/0.3/0.2.

WING: venation similar to *M. nigrohalteralis* (Fig. 2c); CuAx ratio 0.6; lower calypter and haltere yellow.

ABDOMEN: dark metallic green-bronze with grey pruinosity and with short black setulae; hypopygium dark brown with yellowish cerci (Fig. 15f); epandrium oblong; hypandrium and aedeagus simple; epandrial seta short, positioned internally midway between epandrial lobes and base of hypandrium; pedicel of distal epandrial lobe very strong, 2–3 times larger than that of proximal lobe; surstylus fused to epandrium, undivided, U-shaped, and with distal setae as figured; basal section of cercus with single ventral seta and usual dorsal setae; distal cercus elongate, curved, and divided into 3 overlapping sections, the middle section distally expanded and prolonged beyond others.

Female: similar to male except as noted: lacking orientated silvery pruinosity and hairs on pleurae, tibiae and femora.

Remarks. *Medetera austrofemoralis* is known from southern Queensland and the Cape York Peninsula. The dense silvery pruinosity and pilosity on the pleura and legs II and III are a distinctive MSSC. This contrasting pattern has its full effect when the fly is viewed anteriorly with the legs held out from the body.

Medetera salomonis Parent

Medetera Salomonis Parent, 1941: 233.

Type material. HOLOTYPE ♀, PARATYPES 3♀♀: **Solomon Islands:** Guadalcanal, Rere, 18 Aug 1934, R. A. Lever. PARATYPES: 2♀♀, Russell Island, Pepesata, 10 Nov 1934, R. A. Lever (BMNH, examined).

Additional material. (All BPBM except where noted) **American Samoa:** Tutuila: Taputimu Farm, 30 Oct 1964, 19 Aug 1964; Taputimu, 13 Oct 1954. **Australia:** New South Wales: Coffs Harbour, on trunk *Eucalyptus* sp., 24 Oct 1980 (AMS). Northern Territory:(♀ only) Nourlangie Creek, north of Mt Cahill, 19 Nov 1974 (ANIC). Queensland: Atherton, 7 March 1964 (UQIC); Torres Strait, Sue Island, 17–23 May 1983 (QDPI). **Fiji:** Viti Levu, Lautoka, 3 July 1914 (BMNH); Ovalau, Levuka, 10 July 1938. **French Polynesia:** Austral Islands: Rurutu, near Moerai, 90 m, 24 July 1934. Marquesas Islands: Vaipae Valley, Uahuka, Putatauua, 370 m, 20 Sept 1929. Society Islands: Tahiti, Papara District, 23 Feb 1926. **Indonesia:** Irian Jaya: Nabire, Geelvinck Bay, 2 July to 7 Sept 1963; Hollandia-Binnen, 100 m, 31 Oct 1958; Star Mtns, Sibil Valley, 1245 m, Oct-Nov 1961; Vogelkop, Manokauri, 75 m, 19 July 1957; mouth of River Tor, east of Maffen, 2–5 July 1959. **Papua New Guinea:** New Britain: Malmalwan Vunakanau, Gazelle Pen., 11–13 May 1956; Rabaul, no date (USNM). Rossel Island, Abaletic, 0–50 m, 27 Sept 1956 (AMNH); Fergusson Island, Gomwa Bay, Deidei, 2–6 July 1956 (AMNH); Morobe District, Wau, 1150–1250 m, 14 Feb 1963, 25 March 1968; Busu River, north-east of Lae, Sangeman Village, 30 July 1957; Mendi, south Highlands, 1660 m, 13 Oct 1958. **Philippines:** Mindanao, Cotabato Province, General Santos, 15 Aug 1958; Kidpawan, 18 Aug 1958. Sulu, Jolo Island, Talipo, 15–30 m, 31 Aug 1958; Bukidon, Malaybalay, Alanib, 910 m, 25 Oct 1959; Camirines Sur, Mt Isarog, 750–800 m, 26 April 1963; Albay Province, Libon, Caguscos, 200 m, 20 May 1965. **Solomon Islands:** Guadalcanal: Kukum, near Honiara; Tambalia; mouth of Matanikau River; Honiara. San Cristobal: Kira Kira, Maniata; Napagiwae. Rennell Island, Hutuna (ZMUC). Santa Isabel: Tatamba, 0–50 m; Buala. Choiseul: Kolombangara River, 80 m. Malaita: Dala. Vella Lavella: Gingola, 60 m. Florida Group: Vunuka, Small Nggela. (Solomon Island collection dates: Feb to Oct, inclusive). **Tokelau Islands:** Tokelau, 2 m, 1 March 1955. **Vanuatu:** Epi Island, Vaemali, 100–150 m, 8 July to 20 Aug 1967. **Western Samoa:** Upolu: Afiamalu, March, 1962 (MCZ); Utumapu, 14 July (BMNH); Apia, Feb 1955; Fagatogo, 1 May, 9 Nov 1953. (147 specimens examined).

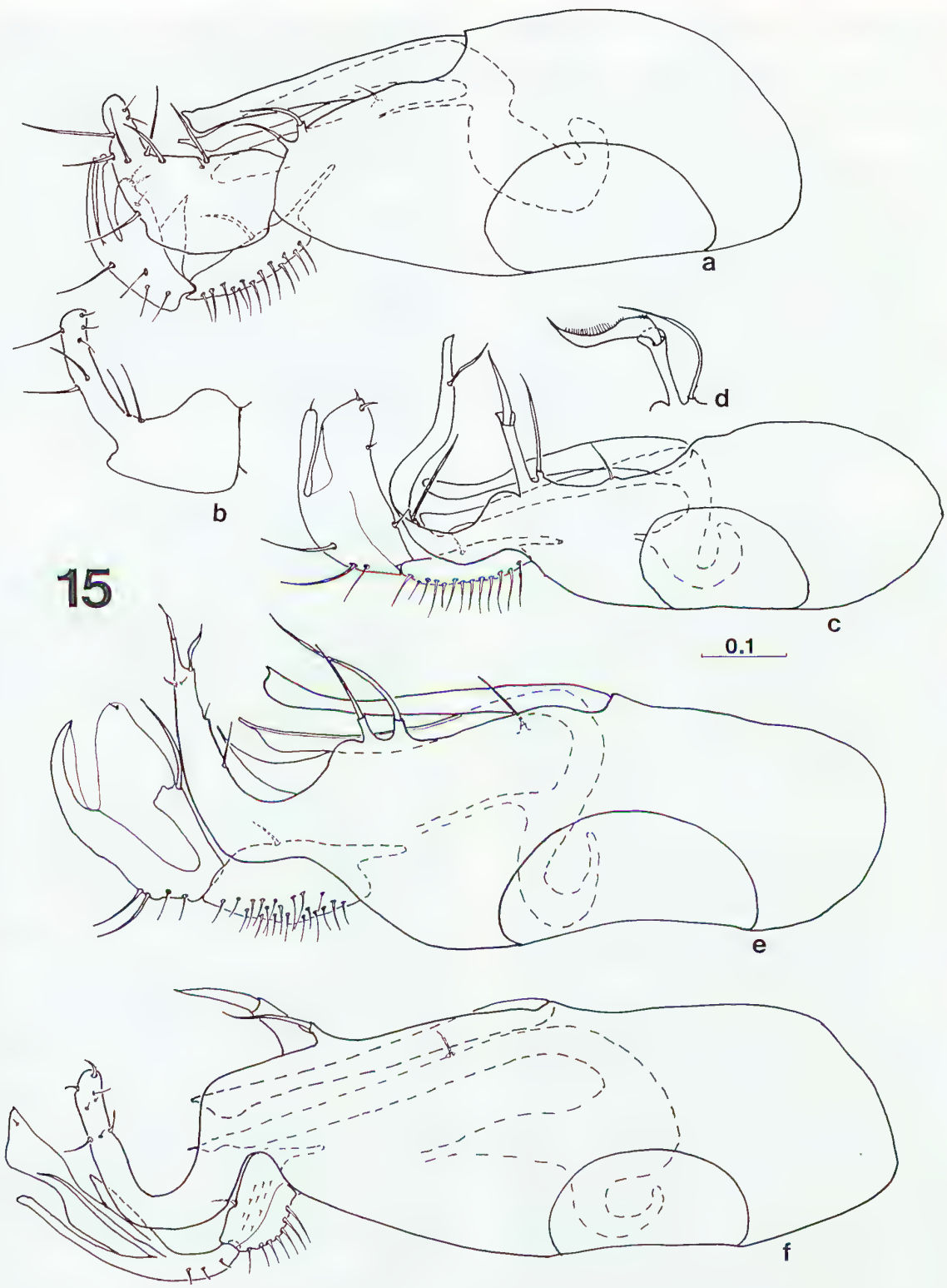

Fig. 15. a–b, *M. salomonis;* a, Malaita, Solomon Islands, hypopygium, left lateral view; b, Atherton, Queensland, surstylus, left lateral view. **c–d,** *M. pseudofemoralis;* c, Wau, Papua New Guinea, hypopygium, left lateral view; d, San Cristobal, Solomon Islands, epandrial lobes, left lateral view. **e,** *M. femoralis,* New Britain; hypopygium, left lateral view. **f,** *M. austrofemoralis,* Lagwi, Queensland; hypopygium, left lateral view.

Description. Male: length 2.5–2.8; wing dimensions 2.5 x 0.7.

HEAD: vertex, frons, face, clypeus metallic green, covered with grey pruinosity, although clypeus with less pruinosity; proboscis brown; scape and pedicel yellow to orange; 1st flagellomere black, subrectangular; arista about as long as head height.

THORAX: dorsum dark metallic green with bronze reflections and with dusting of brown pruinosity; pleura covered with dense grey pruinosity; ac increasing in length posteriorly, posteriormost about as long as width of ac band; 4 strong dc, decreasing in size anteriorly, and with short setulae anteriormost; lateral scutellars less than ⅓ length of medians.

LEGS: coxae and femora black, with femoral 'knees' yellowish; remainder of legs yellowish to infuscated; relative podomere ratios as I: 2.0; 1.7; 0.9/0.6/0.4/0.2/0.3; II: 2.1; 1.9; 1.1/0.6/0.4/0.3/0.2; TII with strong ad-pd pair at ¼; III: 2.0; 2.4; 0.5/1.1/0.6/0.3/0.2.

WING: venation distinctive, with M and R_{4+5} somewhat bowed (Fig. 2b); CuAx ratio 0.6; lower calypter yellow with fan of pale setae; haltere yellow.

ABDOMEN: dark metallic green-bronze with short black setulae; hypopygium dark brown with yellowish cerci (Fig. 15a–b); epandrium ovate; hypandrium and aedeagus simple; epandrial seta short, positioned midway between epandrial lobes and base of hypandrium; epandrial lobes positioned near join with surstylus, subequal with collar-like bases bearing short bristles; surstylus with membranous attachment to epandrium; cuticular projection extending along ventrolateral wall of genital chamber adjacent to epandrial lobes and base of surstylus; surstylus single as single fused curved arm bearing 3 strong ventral setae and strong outer seta as figured (also see 'Remarks', below); cercus divided into basal section articulated with expanded distal section; basal section with strong ventral seta; distal section with ventrobasal triangular structure, midventral lobe with setae as figured, and 2 outer elongate finger-like projections; the distal cercus is freely articulated and can fold back on basal section similar to pocket-knife blade.

Female: similar to male but lacks MSSC.

Remarks. *Medetera salomonis* has a wide distribution across the Pacific, from New Guinea and the Philippines, east through the Solomons, Vanuatu, Fiji, Samoa and French Polynesia, Tokelau, and northern and eastern coastal Australia (Fig. 24).

Medetera salomonis shows some variation in surstylar shape across its range. The characteristic shape from the Solomon Islands, has the surstylus with a broad base and a stout distal arm, and three strong setae along ventral margin (Fig. 15a). In an extreme form from Atherton, Queensland (Fig. 15b), the distal arm is prolonged, only 2 strong ventral setae are present, a ventral mound is present near the base of the surstylus and a distinct dorsal bump is present. Variation in the surstylus occurs variously throughout the range of *M. salomonis:* Philippine, most Papua New Guinean, Samoan, and most French Polynesian specimens similar to the Solomon Island form (Fig. 15a); Wau, Papua New Guinean specimens similar to Fig. 15a but with only 2 strong ventral setae; Hollandia, Irian Jaya, specimens have an elongate arm similar to Fig. 15b but with 3 strong ventral setae; Nabire, Irian Jaya, specimens similar to Fig. 15b but lack dorsal bump; Torres Straits, Queensland, New South Wales and some specimens from the Marquesas display a surstylar form similar to Fig. 15b. I regard the above variations as intraspecific, with various trends in surstylar configuration developing independently across the wide range of *M. salomonis.* In all specimens, the distinctive cercal configuration is identical, as are details of the general habitus. I do not believe these various forms have speciated, but that they might represent peripheral isolates, perhaps forerunners of incipient speciation.

Medetera femoralis Becker

Medetera femoralis Becker, 1922: 52.

Type material. Becker described *Medetera femoralis* from a single male taken at Stephansort, Astrolabe Bay, Papua New Guinea. The holotye, which was deposited at the Hungarian National Museum, Budapest, has since been destroyed. However, the description was accurate enough to enable recognition of the species and I have designated the following male neotype: **Papua New Guinea:** Wau, 1100 m, 25 March 1968, P. Colman (BPBM).

Additional material. Papua New Guinea: Wau, 1200–1250 m, 14 Aug 1976, 14 Feb 1963 (BPBM, USNM); Dreikikir, East Sepik Province, 350 m, 22–25 June 1961 (BPBM); Siutmeri, Sepik River, 16 March 1964 (ANIC); Sangeman Village, near Busu River, north-east of Lae, 30 Aug 1957 (BPBM); Tsenga, Upper Jimmi Valley, 1200 m, 13 Aug 1955 (BPBM). New Britain, Gazelle Peninsula, Malmalwan-Vunakanau, 11–13 May 1956 (BPBM); (12♂♂, 7♀♀ specimens examined).

Description. Male: length 2.8–2.9; wing dimensions 2.7 x 1.0.

HEAD: vertex, frons bright metallic green with some grey pruinosity; face, clypeus metallic green covered with bright dense silvery pruinosity; proboscis dark brown; scape and pedicel yellow; 1st flagellomere brown; arista about as long as head height.

THORAX: bright metallic green with bronze reflections and dusting of grey pruinosity; pleura with silvery pruinosity, evident when viewed anteriorly in an arc 45 degrees either side of median sagittal plane; ac shorter than width of ac band; 4 strong dc, decreasing in size anteriad, and with short setulae anteriormost; lateral scutellars about ¾ length of medians.

LEGS: coxa black, coxa I with dense bright silvery pruinosity; coxae II and III with some grey pruinosity; femora dark brown; tibiae yellowish; basal tarsomeres yellow, distal tarsomeres dark brown; relative podomere ratios as I: 2.9; 2.0; 1.1/0.5/

0.4/0.3/0.3; FI with long black posteroventral setae (MSSC); II: 2.6; 2.3; 1.4/0.7/0.4/0.2/0.2; FII with row of 7–8 black spinelike ventral setae, ending abruptly at 6/10 (MSSC); III: 3.0; 3.3; 0.7/1.7/1.0/0.3/0.2.

WING: membrane somewhat milky, veins brown; M almost straight, gradually approaching R_{4+5} (Fig. 2a); CuAx ratio 0.8; lower calypter and haltere yellow.

ABDOMEN: bright metallic green with bronze reflections, and with short black setulae; sterna with some silvery pruinosity; hypopygium dark brown with yellowish cerci (Fig. 15e); epandrium elongate; hypandrium distally outcurved with ventroapical point; aedeagus simple, tapering near apex; epandrial seta strong, near base of hypandrium; each epandrial lobe bearing stout bristle; tapering side lamella arising from lateral wall of genital chamber near bases of epandrial lobes; surstylus fused to epandrium; surstylus fused into single arm, strongly curved ventrally, and tapering with apical blade-like seta and other setae as figured; basal section of cercus with single ventral seta and usual dorsal setae; distal cercus greatly expanded with strong ventral seta and some dorsal setae, and with strong outer arm adjacent to large weakly sclerotized plate which bears 2 short apical setae.

Female: similar to male; also with bright silvery pruinosity on pleurae and coxa I; lacking posteroventral setae on FI and spine-like setae on FII.

Remarks. *Medetera femoralis* is a distinctive species found in New Guinea and the Bismark Archipelago.

Medetera pseudofemoralis n. sp.

Type material. HOLOTYPE ♂: **Papua New Guinea:** Wau, Big Wau Creek, 1300 m, Nov, 1965, J. Sedlacek. PARATYPE: ♂, south-east Biak Island, 1 July 1962; ♂, **Indonesia:** Irian Jaya, Nabire, Geelvink Bay, 1–20 m, 2–9 July 1962 (BPBM).

Additional material. Australia: 1♂, 1♀, Queensland, Mt Webb National Park, 15°04′S 145°07′E, 28–29 Sept 1980 (ANIC). **Solomon Islands:** 1♂, San Cristobal, Napagiwae, 19 Aug 1960 (BPBM).

Description. Male: length 1.9–2.1; wing dimensions 2.0 x 0.6.

HEAD: vertex, frons dark metallic green with bronze reflections, and with some brown pruinosity; face, clypeus satiny metallic green with grey pruinosity laterally; proboscis dark brown; scape and pedicel yellow; 1st flagellomere brown; arista about as long as head height.

THORAX: dorsum metallic green with brownish pruinosity; pleura with dense brown pruinosity; ac about as long as width of ac band; 4 strong dc, decreasing in size anteriorly, and with short setulae anteriormost; lateral scutellars about ¾ length of medians.

LEGS: coxae, femora dark brown; femoral 'knees' and remainder of legs yellowish to infuscated; relative podomere ratios as I: 1.5; 1.3; 0.7/0.3/0.2/0.2/0.1; II: 1.8; 1.6; 0.8/0.4/0.3/0.2/0.1; III: 1.7; 1.9; 0.4/0.8/0.5/0.2/0.2.

WING: venation similar to Fig. 2a; CuAx ratio 0.6–0.8; lower calypter and haltere yellow.

ABDOMEN: metallic green with bronze reflections and with short black setulae; hypopygium black with yellowish cerci (Fig. 15c); epandrium elongate; hypandrium and aedeagus simple; epandrial seta positioned midway between epandrial lobes and base of hypandrium; distal epandrial lobe much larger than basal lobe, with stout, elongate pedicel and strong bristle, which is bent and expanded in specimen from Solomon Islands (Fig. 15d); side lamella not evident; surstylus fused to epandrium, is twisted and curved, ribbon-like, and bears strong setae as figured; basal cercus with strong ventral setae; distal cercus greatly expanded with large lobate basal portion and narrow outer arm, and with distinctive setae as figured.

Female: similar to male but lacks MSSC.

Remarks. *Medetera pseudofemoralis* is found from New Guinea to the Solomon Islands, and northern Queensland. The Solomon Island specimen is somewhat larger than specimens from New Guinea and Australia, and its distal epandrial lobe bears a curved and expanded blade-like bristle with tiny hairs along its outer margin (Fig. 15d). However, in all other respects the Solomon Island specimen is identical with the New Guinea and Australian specimens, down to details of setation on the surstylus and outer cercus. I therefore regard the Solomon Island specimen as a local variant of *M. pseudofemoralis*.

The *apicalis* Group

The *apicalis* group is defined by the following features: four strong dc usually present which decrease in size anteriorly; hypopygium elongate, subrectangular in lateral view; epandrial lobes separate, with short collar-like bases; epandrial seta present; hypandrium often forming an elongate inverted trough over aedeagus and often held out at an angle from epandrium (e.g. see Figs 17h, 16e); aedeagus, as it emerges from epandrium often appears clasped by base of hypandrium; surstylus fused almost to apex; surstylus usually bearing a distinctive curved, frayed seta on ventral surface (autapomorphy); cerci usually with flattened apicodorsal unguiform seta.

The *apicalis* group is most diverse in the holarctic region (see Bickel, 1985). The nine species considered below include the widespread Indo-Pacific 'tramp' species, *M. austroapicalis*, and five Oriental species: *M. pumila, M. chandleri, M. apicipes, M. longitarsis* and *M. liwo*. Three species are described from Nepal, on the southern slopes of the Himalayas: *M.*

nepalensis, *M. himalayensis* and *M. stomias*. *Medetera nudicoxa* Becker (not seen) described from Darjeeling, India, is probably closely related to *M. himalayensis*.

Medetera austroapicalis n. sp.

Type material. HOLOTYPE ♂, PARATYPES 2♂♂,1♀: **Solomon Islands:** Roroni, 35 km east of Honiara, 7 May 1964, 10 m, R. Straatmann (BPBM).

Additional material. (All BPBM except where noted) **Australia:** New South Wales: Iluka rainforest, Clarence River, 24 Nov 1970, 22 Feb 1965 (AMS). Queensland: 1 km southeast of Mt Cook, 15°30'S 145°16'E, 13 Oct 1980 (ANIC). **Hong Kong:** Taipoka, 30 June 1964. **India:** Yercaud, near Salem, 4500 ft, 6–10 April 1962 (CNC). **Nepal:** Godavari, Katmandu, 5400 ft, 2 July 1967 (CNC). **Papua New Guinea:** Adelbert Mtns, Wanuma, 800–1000 m, 27 Oct 1958; New Britain, Gazelle Peninsula, 4–13 May 1956. **Philippines:** Negros Is,Camp Lookout, Dumaguete, 15 Feb to 15 April 1961 (AMNH); Camarines Sur, Mt Isarog, 750–800 m, 26 April 1963; Ifugao Province, Liwo, 8 km east Mayoyao; 1000–1300 m, 12 June 1967. **Solomon Islands:** Vella Lavella, Ulo Crater, 17 Dec 1963; Vella Lavella, Pusisama, 17 Nov 1963; Santa Ysabel, south-east Tatamba, 8 Sept 1964. **Sri Lanka:** Kohuwala W.P., 16 July 1966 (CNC). (17♂♂, 11♀♀ specimens examined).

Description. Male: length 2.0–2.2; wing dimensions 1.8 x 0.6.

HEAD: vertex, frons, face, clypeus metallic green, with grey pruinosity; proboscis brown; scape and pedicel usually yellow, but sometimes strongly infuscated, appearing brown in some specimens; 1st flagellomere black; arista about as long as head height.

THORAX: metallic green with bronze reflections with some grey pruinosity on dorsum and heavy pruinosity on pleura; setae black; ac increasing in size posteriorly; lateral scutellars ¾ length of medians.

LEGS: coxae, basal ⅔ of femora dark brown to black; remainder of legs yellowish except for brown distal tarsomeres; I: 2.0; 1.5; 0.6/0.4/0.3/0.2/0.2; II: 2.1; 1.8; 0.9/0.4/0.3/0.2/0.2; III: 2.2; 2.5; 0.5/0.8/0.4/0.3/0.2.

WING: M gradually approaches R_{4+5} (Fig. 2f); CuAx ratio 0.8; lower calypters yellow with fan of pale setae; haltere yellow to slightly infuscated.

ABDOMEN: dark metallic bronze-green with short black setulae; hypopygium dark brown with yellowish cerci (Fig. 16e); hypandrium simple, slightly expanded distally; aedeagus with distinctive spurred apex; epandrial seta positioned basad along ventral margin of genital chamber; epandrial lobes as separate short collars, each bearing strong bristle; surstylus fused almost to apex, with curved, distally frayed, ventral subapical seta; cercus stout, with strong curved dorsoapical seta, subtended ventrally by subrectangular cuticular projection and lateral leaf-like seta.

Female: similar to male.

Remarks. *Medetera austroapicalis* has the following distribution: Sri Lanka and India, through south-east Asia to the Philippines, New Guinea and the Solomons, and eastern coastal Australia to northern New South Wales. This species is closely related to the widespread holarctic *M. apicalis*, from which it may be separated by the distinctive aedeagal apex and somewhat smaller size (see Bickel, 1985 for discussion of the somewhat variable *M. apicalis*). *Medetera austroapicalis* probably arose as a southern outlier of *M. apicalis*. The scape and pedicel of *M. austroapicalis* are distinctly yellow in most specimens, although they are sometimes infuscated to a dark brown, especially noted in specimens from southern India and Sri Lanka. However, the hypopygium is identical in both yellow and brown antennal forms and thus are regarded as conspecific. A similar colour variation exists among specimens of *M. apicalis* from the south-eastern United States.

The male specimen from Nepal shows characters intermediate between *M. austroapicalis* and *M. apicalis*. It has brown antennae, only a weak spur on the apex of the aedeagus, the basal epandrial bristle stronger than the distal, and a relatively long epandrial seta. *Medetera austroapicalis* and *M. apicalis* are possibly conspecific, or form a widely distributed somewhat polytypic complex of sibling species. It is difficult to resolve this problem at the morphological level alone.

Medetera chandleri n. sp.

Type material. HOLOTYPE ♂: **Sri Lanka:** Labugama, on tree trunk, 18 Feb 1974, P. J. Chandler (ex. personal collection P. J. Chandler, deposited BMNH).

Description. Male: length 3.0; wing dimensions 2.3 x 0.8; similar to *M. austroapicalis* except as noted.

HEAD: scape and pedicel yellow.

WING: CuAx ratio 0.8; haltere yellow.

ABDOMEN: dark metallic bronze-green with short black setulae; hypopygium dark brown with yellowish cerci (Fig. 16d); hypandrium simple, slightly expanded distally; aedeagus with curved apex; epandrial seta relatively long, positioned midway between epandrial lobe and base of hypandrium; bristles of epandrial lobes strong and arising separately from epandrial margin near base of surstylus; surstylus expanded dorsally, with cuticular striae, and with curved, frayed, subapical ventral seta; cercus with strong curved blade-like dorsoapical seta, subtended ventrally by 2 blade-like setae, curled pedunculate seta, and longer straight pedunculate seta.

Female: unknown.

Remarks. *Medetera chandleri* is known only from Sri Lanka. It is probably derived from *M. austroapicalis*.

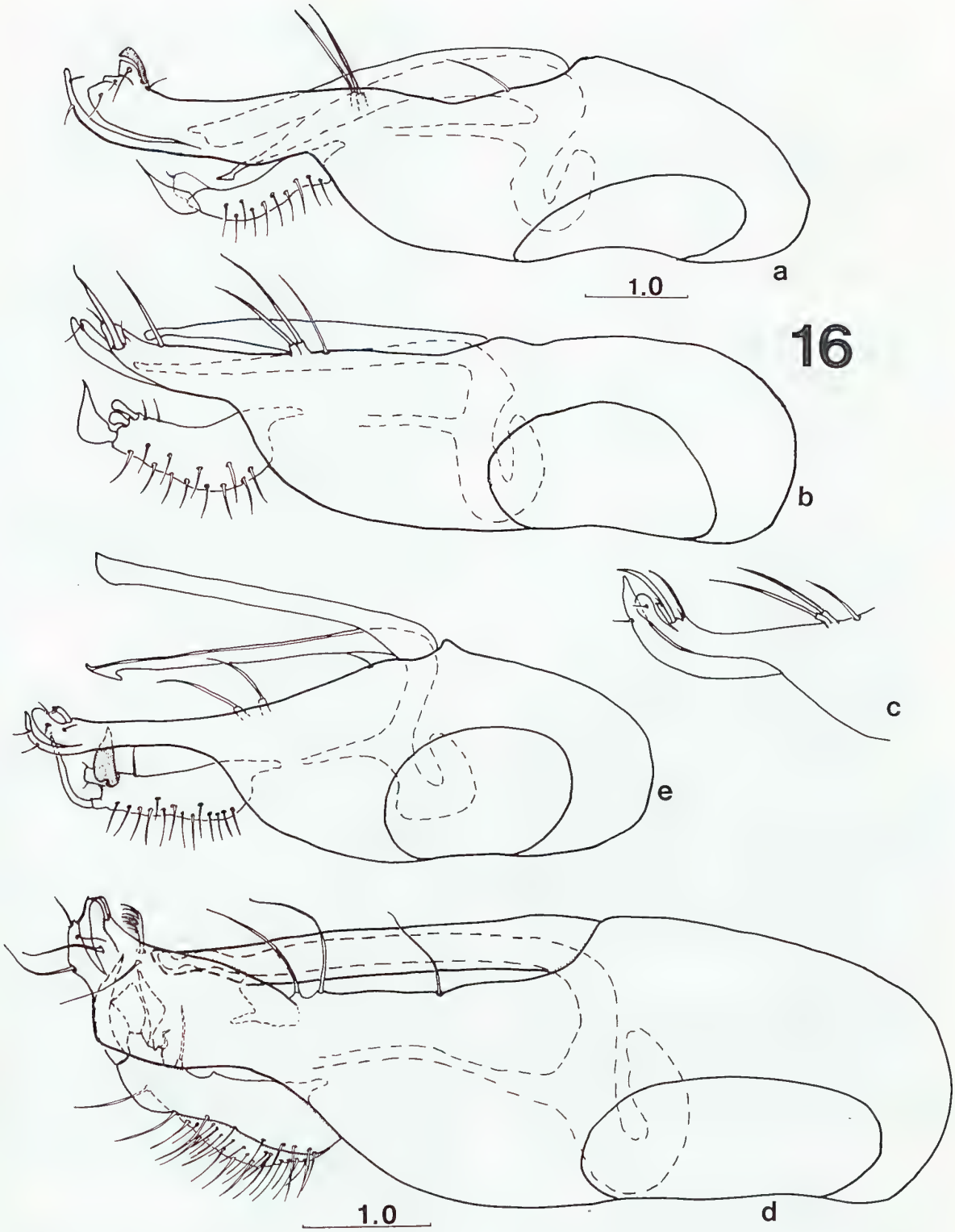

Fig. 16. a, *M. liwo,* Ifuago Province, Philippines; hypopygium, left lateral view. **b,** *M. longitarsis,* Java; hypopygium, left lateral view. **c,** *M. apicipes,* Java; surstylus, left lateral view. **d,** *M. chandleri,* Sri Lanka; hypopygium, left lateral view. **e,** *M. austroapicalis,* Guadalcanal, Solomon Islands; hypopygium, left lateral view.

Medetera pumila de Meijere

Medeterus pumilus de Meijere, 1916: 260.

Type material. SYNTYPES: **Indonesia:** Java, 1♂, 1♀, Batavia, March, 1908; 1♂, Semarang, Sept 1905; E. Jacobson. ♂, labelled "Batavia/ iii 1908 /E. Jacobson", is here designated as LECTOTYPE (ZMUA, examined).

Additional material. Indonesia: 1♂, Sumatra, Pau Bev, Sept 1914 (ZMUA). **Singapore:** 4 June 1985 (CED). **Sri Lanka:** 2♂♂, 3♀♀, Nugegoda W. P., 19 July to 5 Sept 1967; 1♂, 5♀♀, Colombo W.P., 5 Sept 1967; 1♂, Kohuwala W. P., 16 July 1966 (CNC).

Description. Male: length 1.9–2.0; wing dimensions 1.6 x 0.6; similar to *M. austroapicalis* except as noted.

HEAD: face shining metallic blue-green; scape and pedicel yellow, 1st flagellomere brown.

SILVERY PRUINOSITY: orientated pruinosity which appears bright silvery when viewed at an angle of 0–45 degrees either side of median sagittal plane are present as following: anterior coxae I and II, stripe across pleura just above coxae, and lateral margins of abdominal terga 1.

THORAX: all setae yellow; ac short, length less than width of row; lateral scutellars reduced to weak hairs, less than ⅕ length of medians.

LEGS: coxae and legs entirely yellow although coxae II and III somewhat infuscated; I:1.8; 1.6; 0.5/0.5/0.4/0.3/0.2; II: 1.9; 2.0; 0.8/0.7/0.4/0.3/0.2; III: 1.9; 2.1; 0.3/1.0/0.4/0.3/0.2.

WING: CuAx ratio 0.7; haltere pale yellow.

ABDOMEN: metallic bronze-green with short pale setulae; hypopygium dark brown with yellowish cerci (Fig. 17h); hypandrium heavily sclerotized on basal ¾ with 2 upturned short teeth at ¾; hypandrium in distal ¼ appears weakly sclerotized and distinct from basal section; aedeagus deflexed dorsoapically; epandrial seta near base of genital chamber; epandrial lobes separate but adjacent, each bearing a strong bristle; surstylus fused basally, with a strong curved ventral blade-like seta present subapically; cercus with large, weakly sclerotized dorsoapical blade-like seta, subtended by rectangular ventral cuticular projection and distinctive ventral capitate projection.

Female: similar to male.

Remarks. *Medetera pumila* is recorded from Indonesia, Singapore and Sri Lanka, and probably occurs across tropical south-east Asia. The orientated silvery pruinosity of the coxae I and II, pleura and abdominal tergum 1, is similar to that found in members of the *gracilis* group.

Medetera longitarsis de Meijere

Medeterus longitarsis de Meijere, 1916: 262.

Type material. SYNTYPES: **Indonesia:** Java, 2♂♂, Wonosobo, April 1909; 1♂, Nongkodjadjar, Jan 1911, leg. E. Jacobson. ♂, labelled "Wonsobo/ iv 1909/ E. Jacobson" is here designated as LECTOTYPE (ZMUA, examined).

Description. Male: length 3.2–3.3; wing dimensions 3.2 x 1.1; similar to *M. austroapicalis* except as noted.

HEAD: proboscis and antenna black.

LEGS: coxae, femora dark brown; distal ⅙ of femora and remainder of legs yellowish; I: 3.2; 3.4; 1.6/1.9/1.0/0.5/0.4; II: 3.7; 4.4; 2.4/2.7/1.7/0.6/0.4; III: 4.0; 5.6; 0.8/3.3/2.0/0.7/0.4.

WING: M arches gradually towards R_{4+5}; CuAx ratio 1.0.

ABDOMEN: metallic green with bronze reflections; hypopygium dark brown, elongate, subrectangular (Fig. 16b); hypandrium and aedeagus elongate, tapering; epandrial seta long, positioned distally, near epandrial lobes; epandrial lobes adjacent but separate, each bearing a strong bristle; ventral surstylar arm relatively short, bearing stout blade-like seta and long ventral seta; cercus broad, curved, with strong blade-like dorsoapical seta which is subtended by 2 short spatulate setae.

Female: unknown.

Remarks. *Medetera longitarsis* is known only from Java. On the three male specimens, tarsomere 2 is longer than the adjacent tarsomere 1 on all legs, a relationship unique among *Medetera* species.(Also, see 'Remarks' under *M. apicipes*).

Medetera apicipes de Meijere

Medeterus apicipes de Meijere, 1916: 262.

Type material. SYNTYPES 1♂, 2♀♀: Indonesia: Java, Semarang, Sept 1905, E. Jacobson. The male, bearing the label "Semarang/ ix 1905/ Jacobson" is here designated as LECTOTYPE (ZMUA, examined).

Description. Male: length 2.7; wing dimensions 2.7 x 0.8; similar to *M. longitarsis* except as noted.

LEGS: coxae brown; femora yellowish with brownish infuscation; tibiae, basal tarsomeres yellow, distalmost tarsomeres dark brown; I: 2.7; 2.5; 1.1/1.0/0.7/0.5/0.4; II: 2.6; 2.8; 1.8/1.1/0.8/0.7/0.6; III: 2.5; 2.7; 1.9/1.2/0.9/0.4/0.3.

WING: M gradually approaches R_{4+5}; CuAx ratio 0.7; lower calypter yellow with pale setae; haltere yellow.

ABDOMEN: metallic green with bronze reflections; hypopygium similar to *M. longitarsis* except for details of surstylus (Fig. 16c); surstylus deeply cleft, the dorsal surstyla arm with spatulate apex, subtended basad by 2 strong setae as figured; ventral surstylar arm distally curved.

Female: similar to male.

Remarks. *Medetera apicipes* is known only from Java and is closely related to *M. longitarsis*. The two species differ primarily in size, details of surstylar setation, and relative tarsomere ratios.

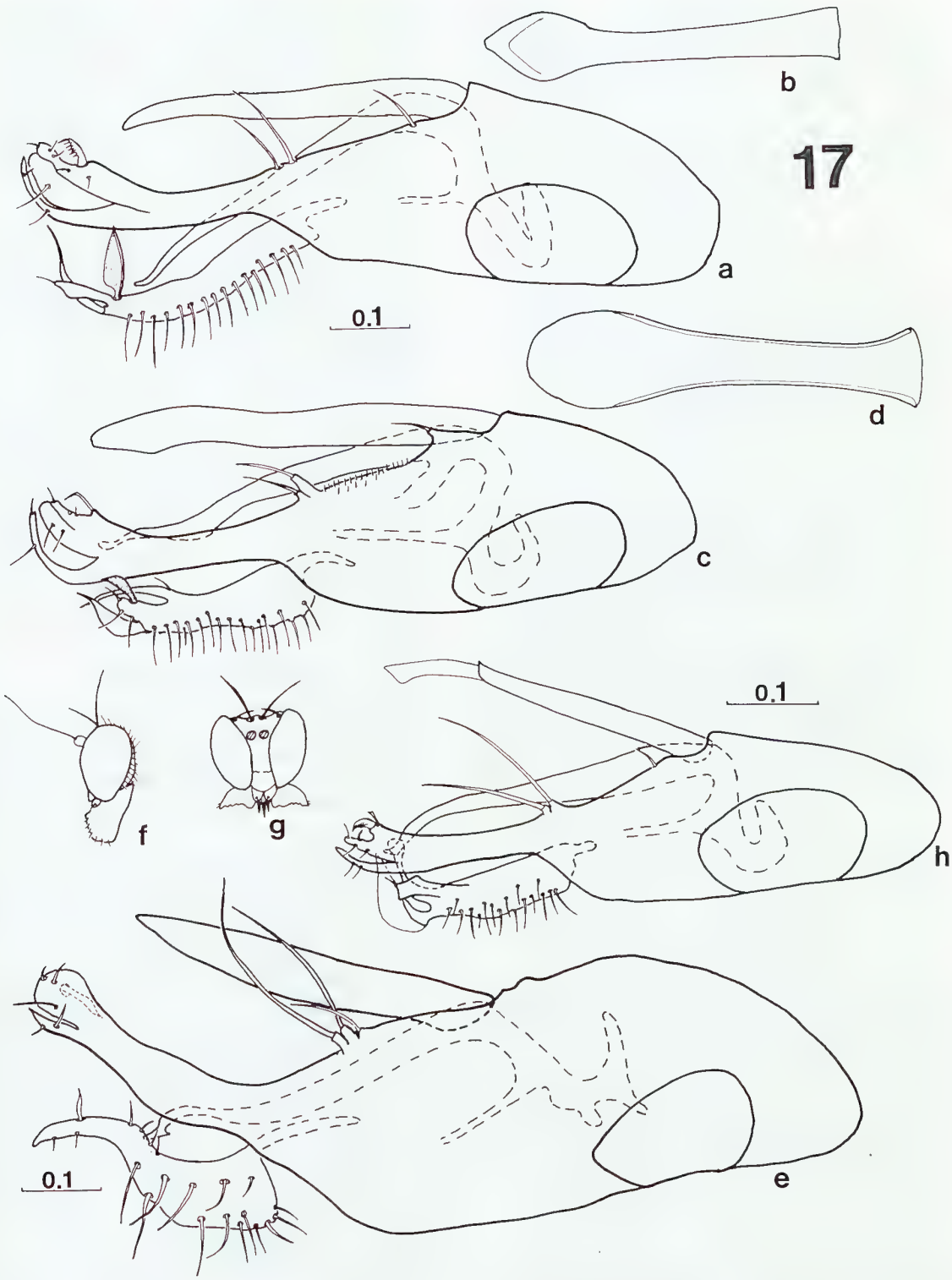

Fig. 17. a–b, *M. nepalensis,* Nepal; a, hypopygium, left lateral view; b, hypandrium, ventral view; **c–d,** *M. himalayensis,* Nepal; c, hypopygium, left lateral view; d, hypandrium, ventral view. **e–g,** *M. stomias,* Nepal; e, hypopygium, left lateral view; f, head, male, left lateral view; g, head, male, anterior view. **h,** *M. pumila,* Sri Lanka; hypopygium, left lateral view;.

Medetera liwo n. sp.

Type material. HOLOTYPE ♂, PARATYPE ♂: **Philippines:** Ifugao Province, Liwo, 8 km east of Mayoyao, 1000–1300 m, 11–12 June 1967, H. M. Torrevillas (BPBM). Both specimens somewhat rubbed and covered with moth scales.

Description. Male: length 1.9; wing dimensions 1.8 x 0.6; similar to *M. austroapicalis* except as noted.

HEAD: vertex, face, frons, clypeus dark metallic green, with dusting of brownish pruinosity; antenna dark brown; arista about as long as head height.

THORAX: dark metallic green with dusting of brownish pruinosity; setae black; scutellars missing.

LEGS: (leg I and most of leg II missing from specimens); coxae and femora black; tibia and tarsis of leg III dark brown; III: 1.6; 1.9; 0.4/0.7/0.4/0.3/0.2/0.2; FIII with pale hairs ventrally.

WING: M gradually approaching R_{4+5}, as in wing of *M. minima* (see Fig. 2i); CuAx ratio 0.6; lower calypter yellow with distinct brown rim and yellow setae.

ABDOMEN: black with metallic green and bronze reflections; segment 7 (peduncle) relatively long, about as long as length of epandrium from base to insertion of cercus; hypopygium dark brown with yellowish cerci (Fig. 16a); hypandrium and aedeagus elongate; epandrial seta positioned basad along ventral margin of genital chamber; epandrial lobes adjacent but separate, collar-like, each bearing strong bristle; surstylus with deep cleft; ventral surstylar arm stout with curved expanded seta; dorsal surstylar arm thin, curving distad of ventral arm; cercus with apical blade-like seta subtended by subrectangular cuticular projection bearing apical seta.

Female: unknown.

Medetera nepalensis n. sp.

Type material. HOLOTYPE ♂, PARATYPE ♀: **Nepal:** 27°57′N 84°59′E, 10,000 ft, malaise trap 5, 18 May 1967, Canadian Nepal Expedition. PARATYPE: ♂, same data but 30 May 1967; (CNC).

Additional material. Probable females of this species: **Nepal:** 27°58′N 85°00′E, 11,200 ft; 27°56′N 85°00′E, 10,000ft; 28°00′N 85°00′E, 9,900 ft; Katmandu, Pulchauki, 8,000 ft; all dates 24 May to 1 June 1967 (CNC).

Description. Male: length 2.7–2.8; wing dimensions 3.2 x 1.2.

HEAD: vertex, frons metallic green, covered with grey pruinosity; face and clypeus coriaceous deep metallic blue-violet, with some pruinosity adjacent to suture; proboscis dark brown; antenna dark brown; 1st flagellomere subrectangular, arista about as long as head height.

THORAX: metallic blue-green, covered with grey pruinosity; brown vittae over ac band and laterally adjacent to dc line, and spreading across anterior half of mesoscutal depression; 5–6 pairs ac, increasing in length posteriorly, the posteriormost pair almost twice the width of ac band; lateral scutellars ⅔ length of medians.

LEGS: coxae and legs dark brown, only distalmost femora yellowish; podomere ratios similar to *M. austroapicalis;* FII and FIII with 5–7 long brown a-v setae.

WING: relatively long and broad compared to body length; wing veins dark brown; venation similar to *M. himalayensis* but without distinct bend in R_{2+3}; CuAx ratio 0.85; lower calypter pale yellow with yellow marginal setae; haltere pale yellow.

ABDOMEN: metallic green-blue with bronze reflections and with short dark setulae, although pale hairs present along edge of tergum 1; hypopygium dark brown with yellowish appendages (Fig. 17a); hypandrium broad, expanded distally in ventral view (Fig. 17b); aedeagus elongate, tapering; epandrial seta positioned basad; epandrial lobes distad, without distinct collar-like bases, but bristles arise directly from margin of epandrium; surstylus elongate, fused basally, expanded and cleft distad; ventral surstylar arm with distinct flattened and frayed seta and with lobes as figured; cercus with apical curved flattened seta, subtended by cuticular projection and subapical ventral blade-like seta.

Female: similar to male, including presence of a-v hairs on FII and FIII.

Remarks. See 'Remarks' under *M. himalayensis.*

Medetera himalayensis n. sp.

Type material. HOLOTYPE ♂: **Nepal:** 27°58′N 85°00′E, malaise trap 3, 11,400 ft, 15 May 1967, Canadian Nepal Expedition (CNC).

Additional material. 3♀♀, probably of this species: **Nepal:** 27°58′N 85°00′E, 11,200 ft, 17 May to 1 June 1967 (CNC).

Description. Male: length 2.4; wing dimensions 2.7 x 1.2; similar to *M. nepalensis* except as noted.

WING: veins dark brown on a milky coloured membrane; R_{2+3} with distinctive bend distally (Fig. 2d).

ABDOMEN: hypandrium in ventral view expanded distally (Fig. 17d); epandrial seta positioned basad on distinct protuberance (Fig. 17c); epandrial lobes adjacent but separate, and basal lobe longer than distal lobe; short setae present along ventral margin between epandrial lobes and epandrial seta; surstylus expanded distally with wedge-shaped cleft; ventral surstylar arm with thin curved seta; cercus with apical blade-like seta subtended by cuticular projection bearing curved flattened seta; cercus with ventral digitiform cuticular projection at ⅔.

Female: similar to male.

Remarks. *Medetera himalayensis* and *M. nepalensis* were both taken at relatively high altitudes in Nepal. They are closely related, differing primarily in size and in details of the hypopygium. Females of the two species cannot be reliably separated. Both

species have relatively long, broad wings, the wing length being distinctly longer than body length (in most *Medetera* species, the wing is shorter or subequal to the body length).

Medetera himalayensis has a distinct bend in wing vein R_{2+3}. *Medetera nudicoxa* Becker (not seen) from Darjeeling, India, is described as having a bend in the third long vein, and the two species could be closely related.

Medetera stomias n. sp.

Type material. HOLOTYPE ♂, PARATYPES 13♂♂, 10♀♀: **Nepal:** 27°56′N 85°00′E, 9,000–10,000 ft, oak forest, malaise trap, 22–29 May 1967. PARATYPES: 19♂♂, 9♀♀, 27°58′N 85°00′E, 11,100–11,400 ft, 21 May to 24 June 1967; 3♂♂, 3♀♀, 28°00′N 85°00′E, 9,900–10,500 ft, 26 May to 1 June 1967; all from Canadian Nepal Expedition (CNC).

Description. Male: length 3.2–3.4; wing dimensions 3.5 x 1.5.

HEAD: vertex, frons dark brown with metallic green-blue reflections, covered with brown pruinosity; face and clypeus shiny dark brown, with blue reflections, divided medianly by thin pruinose strip which is expanded ventrally across frontoclypeal suture and over clypeus; proboscis dark brown, enlarged, projecting ventrally (Fig. 17f); labellae drawn up horizontally in some specimens, flap-like (Fig. 17g), such that 6 dark radial pseudotracheae are visible on pale median surface; antenna red-brown; arista about as long as head height.

THORAX: dorsum dark brown with metallic greenblue reflections; dorsum and pleura covered with dense brown pruinosity; 5–6 pairs ac, about as long as width of ac band, posteriormost pair 1½ length of ac band; lateral scutellars ⅔ length of medians.

LEGS: coxae dark brown, legs red-brown with femora apically yellow; podomere ratios as: I:9.0; 7.5; 3.0/2.0/1.5/1.0/1.0; II:9.0; 10.0; 5.0/3.0/2.5/1.2/1.0; III: 10.0; 13.0; 3.0/5.0/2.5/1.5/1.0.

WING: M gradually rising towards R_{4+5}; CuAx ratio 0.75; lower calypter yellow with fan of black setae; haltere yellow.

ABDOMEN: dark red-brown with metallic green reflections, covered with dusting of grey pruinosity, and with short black setulae; hypopygium dark red-brown with yellowish cerci (Fig. 17e); hypandrium broad in ventral view; aedeagus in lateral view tapering with distinctive spurred apex; epandrial seta on short protuberance adjacent to epandrial lobes; epandrial lobes with short collars and bearing long strong bristles; surstylus fused almost to apex, with shallow apical cleft; surstylus bearing strong blade-like seta mediad; cercus curved and narrowing distally, and bearing setae as figured; cercus lacking blade-like dorsoapical seta.

Female: similar to male, also with distinctive broad proboscis.

Remarks. The large projecting proboscis of *M. stomias* is unique among *Medetera* species. In hypopygial structure, *M. stomias* is very close to the western palearctic *M. cuspidata,* especially in the shape of the cercus (see figures in Negrobov 1971–77), although *M. cuspidata* is much smaller and has a normal proboscis. *Medetera stomias* has long broad wings, similar to those of *M. nepalensis* and *M. himalayensis.* The specific name, *stomias* is Greek for 'large or hardmouthed animal'.

The *diadema-veles* Group

The *diadema-veles* group is characterized by the following features: four strong dc present, decreasing in size anteriorly; TII longer than FII in all species; male basitarsus III with anteroventral tooth near tibial joint (apomorphy); hypopygium pyriform, inflated basally (autapomorphy); epandrial lobes with bases adjacent, partially to completely fused, forming an elongate collar from which the two bristles arise (autapomomorphy); epandrial seta reduced or lost (autapomorphy); surstylus fused almost to tip; dorsal surstylar arm usually extending somewhat beyond the ventral; hypandrium elongate, narrow, tapering (autapomorphy); aedeagus elongate, tapering, usually with a pair of wing-like appendages basally; cercus usually with apical flattened blade-like or unguiform seta.

The *diadema-veles* group is one of the most derived *Medetera* species groups and has radiated extensively in the holarctic region (Bickel, 1985). The two species considered here, *Medetera opaca* and *M. grisescens,* belong to the '*veles* assemblage', having totally lost the epandrial seta and with the bases of the epandrial lobes almost completely fused.

Members of this group have become established in all zoogeographical regions and some, such as the Indo-Pacifc *M. grisescens,* are widespread 'tramp' species.

Medetera opaca de Meijere

Medeterus opacus de Meijere, 1916: 258.

Type material. SYNTYPES: **Indonesia:** Java, 2♂♂, 1♀, Salitiga, May 1909, Docters van Leeuwin; 1♀, Batavia, Jan 1900, E. Jacobson. ♂, bearing the label "Salitiga/ v 1909/ Docters van Leeuwin" is here designated as LECTOTYPE (ZMUA, examined).

Additional material. Hong Kong: 1♂, New Territory, Sai Kung Sta., 4 May 1965. **Vietnam:** 2♂♂, Dalat, 1500 m, 26–27 Sept 1960; 1♀, Ban Me Thout, 500 m, 16–18 May 1960 (BPBM).

Description. Male: length 1.7–1.8; wing dimensions 1.8 x 0.6.

HEAD: vertex, frons, face, clypeus metallic greenblack, covered with dense grey pruinosity; proboscis dark brown; antenna black; arista about as long as head height.

THORAX: dorsum dark metallic green with dense

grey pruinosity; brown vittae present over ac band and laterad over dc bands; 8–9 pairs ac, increasing in length posteriorly; lateral scutellars reduced to short hairs.

LEGS: coxae brown, femora yellow to somewhat infuscated, remainder of legs yellow; podomere ratios as I: 1.6; 1.5; 0.8/0.6/0.4/0.3/0.2; II: 2.0; 2.2; 1.1/0.8/0.5/0.4/0.2; III: 2.2; 2.4; 0.6/1.1/0.6/0.3/0.2.

WING: M gently arches towards R_{4+5}; CuAx ratio 0.8; lower calypter and haltere yellow.

ABDOMEN: black with grey pruinosity; hypopygium dark brown with yellowish cerci (Fig. 18a); aedeagus with subapical swelling; epandrial seta absent; bristles of fused epandrial lobes branched apically; cercus with dorsoapical blade-like seta on stout base, and subtended by ventral lobate projection bearing 2 setae.

Female: similar to male.

Remarks. *Medetera opaca* is found in south-eastern Asia and is distinguished from all other holarctic members of the '*veles* assemblage' by its relatively small size, reduced lateral scutellars, and distinctive cercal structure.

Medetera grisescens de Meijere

Medeterus grisescens de Meijere, 1916: 259.
Medetera hawaiiensis Van Duzee, 1933: 343 (syn. *Medetera atrata*, Hardy & Kohn, 1964: 254), n. syn.
Medetera atrata Van Duzee, 1933: 344, n. syn.
Medetera cilifemorata Van Duzee, 1933: 344, n. syn.
Medetera palmae Hardy, 1939: 351, n. syn.

Type material. De Meijere described *Medeterus grisescens* from 3 SYNTYPES: **Indonesia:** Java: 1♂, Batavia, Oct 1907; 1♀, Batavia, Aug 1907; 1♀, Wonosobo, April 1909; all E. Jacobson; the ♂, bearing the label "Batavia/ x 1909/ Jacobson" is here designated as LECTOTYPE (ZMUA, examined). Van Duzee (1933) designated male HOLOTYPES for *Medetera hawaiiensis*, *M. atrata* and *M. cilifemorata*, all collected on Oahu, Hawaiian Islands. I have examined the 3 holotypes (all BPBM) and regard them as belonging to *M.*

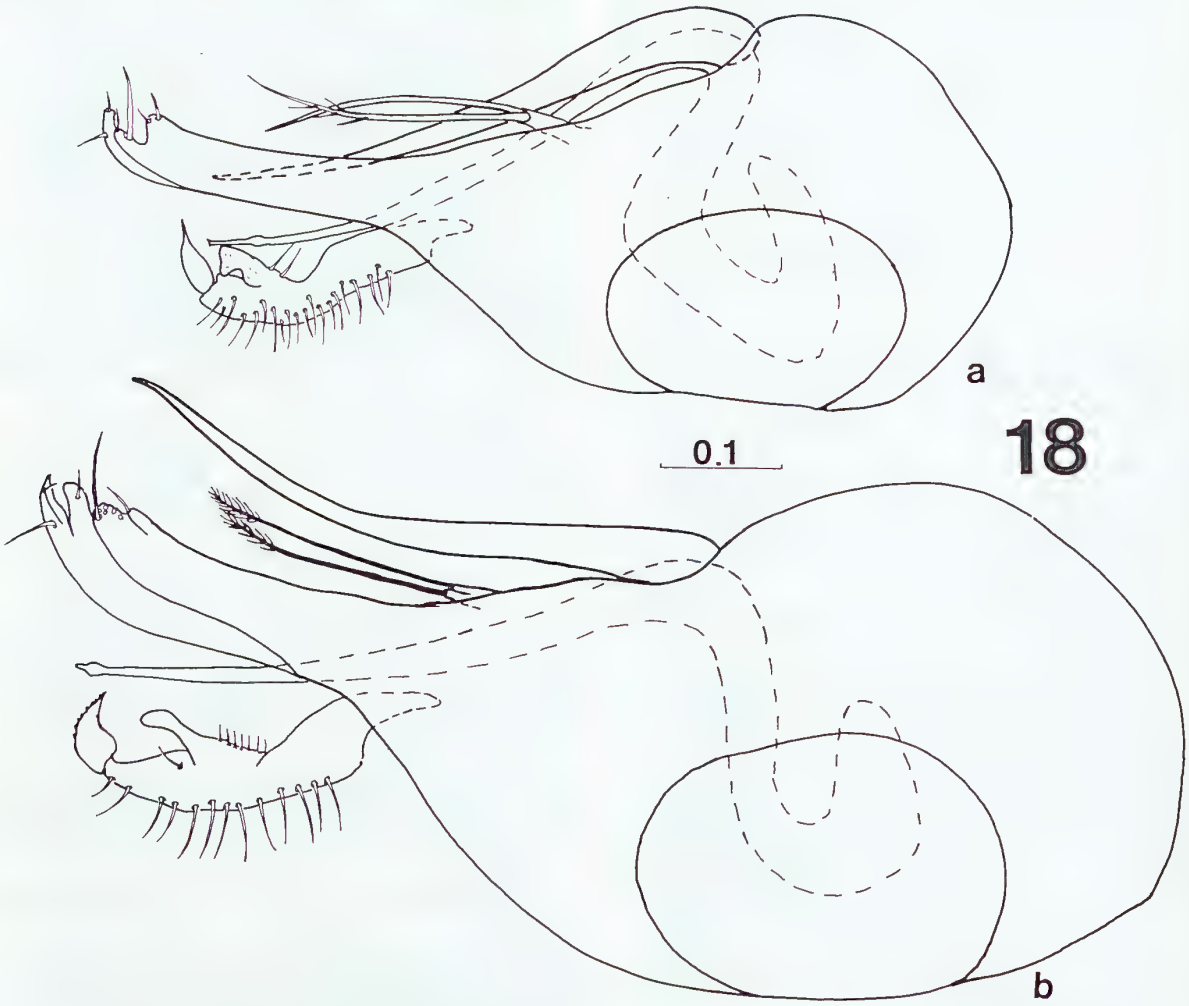

Fig. 18. a, *M. opaca*, Java; hypopygium, left lateral view. **b,** *M. grisescens*, Honolulu, Hawaii; hypopygium, left lateral view.

grisescens. Hardy (1939) described *M. palmae* from specimens collected at Brisbane, Queensland. The types have been lost, but from his description, especially noting the large swollen hypopygial base, I regard this species as a synonym of *M. grisescens*.

Additional material. American Samoa: Tutuila, Taputimus. **Australia:** New South Wales: metropolitan Sydney; Washpool National Park, near Baryugil. Queensland: Biloela; Cooloola National Park; Booloomba Creek, Conondale Ranges; metropolitan Brisbane; Ingham; Peerman; Milla-Milla; Maalan; Townsville; Lamington National Park. **China:** Fukien, Yungan City. **Fiji:** Nadi. **Hawaiian Islands:** Hawaii, Hawaiian Volocanoes National Park; Oahu, Honolulu. **Hong Kong:** New Territory, Lantau Is.; Kowloon, Taipokau. **India:** Silchar Cachar; Bihar Bunhar: Nedungadu, Tenjore; Kodaikanal, Pulney Hills, 1950 m. **Indonesia:** Sumatra, Fort de Kock, 920 m. **Japan:** Ryukyu Islands: Okinawa, Iwa; Ishigaki Is., Banna. **Laos:** Sayaboury. **Malaysia:** Kedah, Kuala Lumpur; Selangor, near Batu Caves. Sabah: Tawau, Quoin Hill; Sarawak: Kuching, Santubong. **Nepal:** Pokhara, 910 m. **New Caledonia:** Noumea. **Seychelles:** Mahe. **Singapore. Sri Lanka:** Colombo W.P.; Nugegoda W.P.; Piliyandala W.P.; Pevadenija; Luduganga. **Taiwan:** Anping; Liukuei, Kaohsiunghsien; Hengchun, Pingtunghsien; Kuraru; Taipei, Yehliu Beach. **Thailand:** Biserat; Chieng Mai Province, Chieng Mai, 300 m. **Western Samoa:** Upolu, Malololelei, 600 m. (285 specimens examined: AMS, ANIC, BMNH, BPBM, CNC, MCZ, QMB, UQIC, USNM).

Description. Male: length 2.7–3.0; wing dimensions 2.8 x 0.7.

HEAD: vertex, frons, face metallic green with grey pruinosity; clypeus satiny metallic blue-green; proboscis dark brown; antenna black.

THORAX: metallic green-bronze with grey-brown pruinosity dorsally and dense grey pruinosity on pleura; bronze vittae present over ac band and laterally over dc bands; mesonotal depression with dense grey pruinosity; ac relatively short, not as long as width of ac band; lateral scutellars about ⅔ length of medians.

LEGS: coxae brown, femora yellow to infuscated, distalmost femora and remainder of legs yellow; podomere ratios as: I: 2.5; 2.3; 1.0/0.8/0.4/0.4/0.3; II: 2.3; 2.6; 1.7/0.8/0.5/0.3/0.2; III: 2.6; 3.4; 0.7/1.6/0.7/0.4/0.3.

WING: venation similar to Fig. 2h; CuAx ratio 0.6; lower calypter and haltere yellow.

ABDOMEN: dark metallic green-bronze with grey pruinosity and short black setulae; hypopygium dark brown with yellowish cerci (Fig. 18b–c); epandrium greatly inflated basally; aedeagus with apical swelling; epandrial seta absent; bases of epandrial lobes almost completely fused; epandrial lobe bristles branched distally; cercus with apical toothed blade-like seta bearing irregular serrations on external surface; cercus with distinctive midventral clavate projection.

Female: similar to male.

Remarks. *Medetera grisescens* has a wide distribution, from the Seychelles, Sri Lanka and the Indian subcontinent, throughout south-east Asia including southern China and the Ryukyu Islands, to coastal eastern Australia and many Pacific islands, including Hawaii (Fig. 21). I have seen no specimens from New Guinea or the Solomon Islands, although I would expect the species to be there, especially around settled regions. The species appears to be absent from New Zealand. *Medetera grisescens* probably originated in the Orient as a southern outlier of the diverse holarctic *diadema-veles* species group. Undoubtedly it has a broad ecological tolerance and is well adapted for dispersal throughout the Indian and Pacific oceans as a 'tramp' species, perhaps aided by human transport. *Medetera grisescens* is often found in large numbers resting on tree trunks in disturbed and settled areas, although it is also found in relatively undisturbed habitats.

Collection dates for *Medetera grisescens* suggest year round adult activity in the humid tropics, with more seasonal occurance in temperate regions. In the Sydney district, for example, *M. grisescens* is common in parks and gardens throughout the warm months from late September to early May, but is not found during the winter months.

Although the femora are usually yellowish, some specimens have distinctly brown femora I and II. Also, the basal tooth of the cercal blade-like seta is more pronounced in some specimens. However, *M. grisescens* maintains a fairly constant facies across its entire range.

The *signaticornis-pinicola* Group

The *signaticornis-pinicola* group is defined by the following features: relatively large species, usually longer than 2.8; scape and pedicel usually yellow; dc 6–10, strong, decreasing anteriorly, and merging into a field of setulae; median and lateral scutellars both strongly developed; hypopygium often large and massive, as large as preabdomen; hypandrium broad, flat; epandrial lobes with separate cylindrical bases, often positioned laterad of each other; epandrial seta present, positioned near base of hypandrium.

The *signaticornis-pinicola* group is a diverse assemblage which is closely associated with the holarctic circumboreal forests and contains many important predators of conifer-attacking Scolytidae (see Bickel, 1985). The single Oriental species considered below, *Medetera kinabaluensis*, from high altitude forests in Borneo, definitely belongs in this species group, and is associated with the *pinicola* subgroup, which in the holarctic region is characterized by the following features: cercus large, often massive, appearing hemispheroidal in dorsal view; epandrium subrectangular in lateral view; aedeagus elongate, tapering, and simple; surstylus broad, massive, with elongate, seta-bearing arms; pair of 'bottle-brush' shaped appendages arising internally from aedeagus (not present on *M. kinabaluensis*).

Medetera kinabaluensis n. sp.

Type material. HOLOTYPE ♂: **Malaysia:** Sabah: Mt Kinabalu, Kambaranga, 2140 m, 31 Oct 1958, T. C. Maa (BPBM).

Additional material. Possible ♀ of this species: **Malaysia:** Sabah: Tenompok, 13 Feb 1959 (BPBM).

Description. Male: length 3.7; wing dimensions 4.0 x 1.5; a large, dark green species.

HEAD: vertex, frons, face, and clypeus metallic green with bronze reflections; face and clypeus with coriaceous texture; proboscis, black, massive; scape and pedicel yellow; 1st flagellomere black; arista about as long as head height.

THORAX: dorsum dark metallic green with bronze reflections, and with thin layer of grey pruinosity; pleura with dense grey pruinosity; setae black; ac strong, and increasing in length posteriorly, the posteriormost twice as long as width of ac band; dc missing, but distinct sockets indicate at least 5–6 strong setae present.

LEGS: entirely black, femoral 'knees' somewhat paler; relative podomere ratios as: I: missing; II: 3.9; 3.7; remainder missing; TII with strong apicoventral seta; III: 3.6; 4.2; 1.0/1.7/1.0/0.5/0.3.

WING: M approaching R_{4+5} in gradual arc, similar to wing of *M. signaticornis* (see Bickel, 1985); CuAx ratio 0.6; lower calypter yellow with dark brown rim, and bearing fan of pale setae; haltere yellow.

ABDOMEN: black with metallic green reflections, and with short black setulae; hypopygium dark brown with yellowish cerci (Fig. 19a); hypandrium in ventral view subrectangular and with pointed apex (Fig. 19b); aedeagus tapering, simple; epandrial seta strong, positioned near base of hypandrium; epandrial lobes with large cylindrical bases, positioned laterad of each other, and each bearing strong bristle; surstylus fused to epandrium; surstylus massive, with ventral cuticular striae, not deeply divided, and bearing distal lobes and setae as figured; cercus expanded and bulbous distally, and bearing 2 distinctive ventral projections; basal ventral projection with 3 apical setae.

Female: similar to male.

Remarks. *Medetera kinabaluensis* is found on high altitude slopes of Mt Kinabalu in Borneo. The presence in Borneo of a member of a circumboreal group is an interesting disjunction which is discussed further under 'Zoogeography'.

Other *Medetera* Species

The following species are phylogenetically somewhat isolated and do not appear to fit into any of the previously described groups.

Medetera minima de Meijere

Medeterus minimus de Meijere, 1916: 259 (nec. *Medetera minima* Van Duzee, 1925 = *M. postminima* Steyskal, 1967: 224).

Type material. SYNTYPES: **Indonesia:** 2♂♂, Java, Depok, Oct 1909, E. Jacobson; Batavia, Feb 1908, E. Jacobson (this specimen is male, not female as described by de Meijere). The male bearing the label "Depok/ x-09/ Jacobson" is here designated LECTOTYPE (ZMUA, examined).

Additional material. Australia: Queensland, Mt Cook National Park, 15°29'S, 145°16'E, 10 May 1981 (ANIC). **Indonesia:** Sumatra, Fort de Kock (ZMUA). Irian Jaya: Biak Island, 22 June to 1 July 1962; Nabire, 5–50 m, 25 Aug

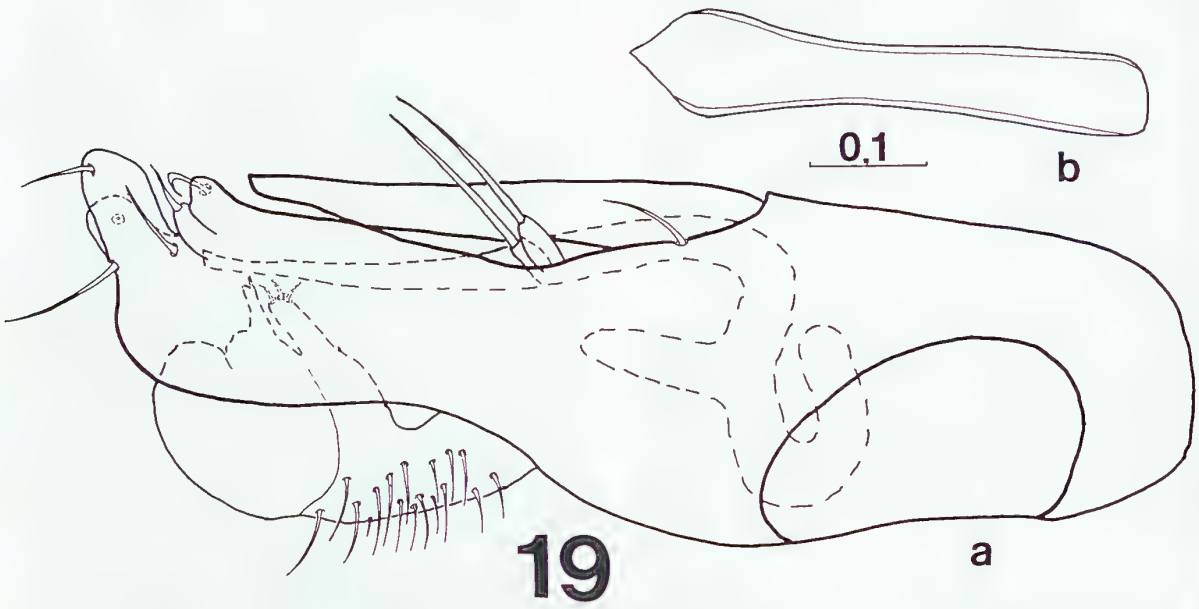

Fig. 19. *M. kinabaluensis*, Sabah; **a**, hypopygium, left lateral view; **b**, hypandrium, ventral view.

to 2 Sept 1962 (BPBM). **Malaysia:** Selangor, Kelang, on tree trunk, 10 March 1982 (BMNH). **Papua New Guinea:** Wau, Hospital Creek, 1250 m, 22 May 1965; Wewak, 2–20 m, 11 Oct 1957; Cape Rodney, 10 m, 3 Nov 1960. New Britain, Linga Linga, west of Willaumez Pen., 15 April 1956 (BPBM). **Solomon Islands:** Santa Isabel, Tatumba, 2 Oct 1965 (BMNH) (12 ♂♂, 3♀♀ specimens examined).

Description. Male: length 1.7–1.8; wing dimensions 1.7 x 0.5.

HEAD: vertex, frons, face, clypeus dark metallic green with brownish pruinosity; proboscis dark brown; antenna black; arista about as long as head height.

THORAX: dorsum dark metallic green with bronze reflections; pleura covered with brownish pruinosity; setae black; 10–12 pairs ac, increasing in length posteriorly, the posteriormost longer than width of ac band; 2 strong dc bordering mesonotal depression, the anterior dc as short setulae; lateral scutellars reduced to weak hairs.

LEGS: coxae, femora black to femoral 'knees'; remainder of legs yellow, with distal-most tarsomeres darkened; relative podomere ratios as I: 1.2; 0.9; 0.4/0.3/0.2/0.2/0.2; II: 1.1; 1.2; 0.6/0.4/0.3/0.2/0.2; TII with single ad at ¼; III: 1.3; 1.4; 0.2/0.6/0.4/0.2/0.2.

WING: M gradually approaches R_{4+5} (Fig. 2i); CuAx ratio 0.5; lower calypter yellow with fan of pale setae; haltere yellow.

ABDOMEN: dark metallic green with short black setulae; hypopygium dark brown with yellowish cerci

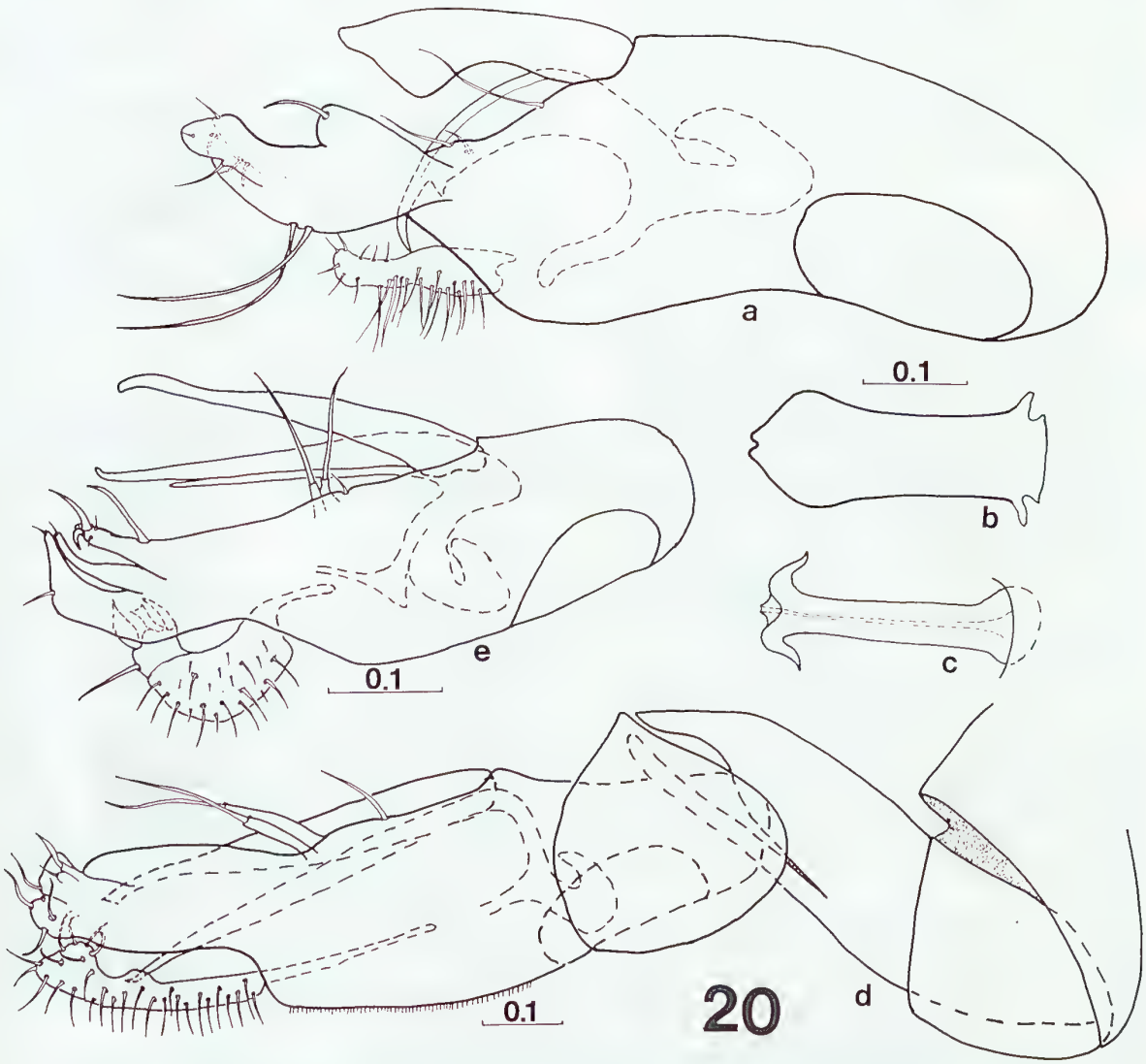

Fig. 20. *M. malaisei,* Kambalti, Burma; **a,** hypopygium, left lateral view; **b,** hypandrium, ventral view; **c,** aedeagus, ventral view; **d,** *M. longa,* Vientiane, Laos, hypopygium, left lateral view; **e,** *M. minima,* Selangor, Malaysia, hypopygium, left lateral view.

(Fig. 20e); hypandrium elongate; aedeagus slightly recurved within epandrium; aedeagus elongate with curved tip and with side lamellae; epandrial seta short, adjacent to epandrial lobes; epandrial lobes each with strong simple bristle; surstylus fused to epandrium; dorsal surstylar arm curved mediad; middle surstylar arm narrow with apical seta; ventral surstylar arm with strong ventral and apical setae; cercus stout, curved, with strong subapical dorsal seta, and with 3 distinctive apical blade-like setae as figured.

Female: similar to male.

Remarks. *Medetera minima* has a distinctive hypopygium and is distributed from Malaysia to the Solomons, including northern Queensland (Fig. 23). This species has certain similarities with the *flaviscutellum* group (cercus with dorsoapical blade-like setae, two strong dc bordering mesoscutal depression). However, the somewhat basal position of the epandrial lobes, fusion of surstylus with epandrium, aedeagus with side lamellae, black antenna, relatively short arista, places the species outside that group.

Medetera malaisei n. sp.

Type material. HOLOTYPE ♂: **Burma:** (N.E.), Kambalti, 7000 ft, 23 May 1934, R. Malaise (BMNH).

Description. Male: length 2.3; wing dimensions 2.4 x 1.1.

HEAD: vertex, frons, face black with metallic green reflections and covered with brown-grey pruinosity; clypeus black; proboscis dark brown; scape black, remainder of antenna missing.

THORAX: black with metallic green reflections, and with some grey pruinosity; pleura covered with dense grey pruinosity; setae black; ac increasing in length posteriorly, posteriormost twice as long as width of ac band; 4 strong dc present, decreasing anteriad, and with much shorter dc and short setulae anteriormost; lateral scutellars ¾ length of medians.

LEGS: coxae, femora black to femoral 'knees'; remainder of legs yellowish with distal tarsomeres darkened; relative podomere ratios as: I: 2.0; 1.9; 0.8/0.4/0.3/0.2/0.2; II: 2.1; 2.2; 1.0/0.5/0.3/0.2/0.2; III: 2.4; 2.6; 0.6/0.8/0.4/0.2/0.2.

WING: relatively broad; M gradually approaches R_{4+5}; CuAx ratio 0.5; lower calypter yellow with fan of pale setae; haltere yellow, but club somewhat infuscated.

ABDOMEN: black with grey pruinosity, and with short black setulae; hypopygium dark brown with yellowish cerci (Fig. 20a); epandrium ovate; hypandrium in ventral view broad, widened subapically, and with apical notch (Fig. 20b); aedeagus in ventral view with subapical backwardly directed hooks, i.e., anchor-shaped (Fig. 20c); epandrial seta very long; epandrial lobes lacking distinct basal pedicels, and only present as 2 setae, distal seta being twice as long as basal; surstylus fused to epandrium, but distinctly narrowed basally; surstylus somewhat clavate, with ventral mound bearing 1 strong seta, 2 very long setae along dorsal margin, and other setae as figured; cercus short, blunt, with setae as figured.

Female: unknown.

Remarks. *Medetera malaisei* is known only from the highlands of north-eastern Burma. It has an unusual hypopygial structure with an anchor-shaped aedeagus, a very long epandrial seta, a short blunt cercus, and epandrial lobes represented only by setae, totally lacking the usual basal pedicels. This species does not appear to be closely related to any other described palearctic or Oriental species.

Medetera longa Negrobov & Thuneberg

Medetera longicauda Becker, 1922: 50 (preocc. Becker 1917).

Medetera longa Negrobov & Thuneberg, 1970: 143 (replacement name for *longicauda* Becker 1922).

Type material. Becker described *M. longicauda* from 2♂♂ and 1♀ syntypes collected at Kankau, Taiwan. One male and one female were deposited in the Hungarian National Museum and have since been destroyed. The other male, deposited at DEI could not be located (G. Morge, letter). In size, colouration, thoracic chaetotaxy, leg length, and structure of the male postabdomen, Becker's original description and figure are similar to the additional Oriental specimens considered below.

Additional material. ♂: **Laos:** Vientiane Province, Gi Sion Valley, De Tha Ngone, 19–26 Dec 1965; 2♀♀, Sayaboury Province, Sayaboury, 12 Dec 1965 (BPBM). Possible ♀♀ of this species: 1♀, **Malaysia:** Pahang, Cameron Highlands, Tanahkalia, 4800 ft (BMNH); 2♀♀, Philippines: Port Bauge, Jan 1915 (ZMH).

Description. Male: length 3.2; wing dimensions 3.6 x 1.4.

HEAD: vertex and frons metallic green-bronze with some grey pruinosity; face shiny metallic blue, with green reflections; clypeus shiny metallic green with bronze reflections; proboscis black, massive; antenna black; arista about as long as head height.

THORAX: dorsum metallic green with bronze reflections and some grey pruinosity; pleura covered with dense grey pruinosity; setae black; ac increasing in length posteriorly, posteriormost as long as width of ac band; 3 strong dc present, sharply decreasing in size anteriorly, and with short setulae anteriormost; lateral scutellars ¾ length of medians; 8–10 long pale ppls present.

LEGS: relatively long; coxae black; remainder of legs yellow with only distal tarsomeres darkened; relative podomere ratios as: I: 3.4; 3.6; 1.9/2.1/1.5/0.7/0.4; II: 3.5; 4.6; 3.8/2.2/1.5/0.6/0.4; III: 3.5; 5.8; 1.3/3.3/1.6/0.4/0.4.

WING: venation similar to Fig. 2h; CuAx ratio 1.0; lower calypter and haltere yellow.

ABDOMEN: dark metallic green-bronze with short

pale setulae; tergum 6 short; segment 7 very long, about as long as epandrium, fused basally and deeply cleft distally near attachment with sternum 8 (Fig. 20d); hypopygium dark brown with yellowish cerci; epandrium elongate, subrectangular; hypandrium and aedeagus elongate, tapering and simple; epandrial seta strong, positioned almost midway between epandrial lobes and base of hypandrium; epandrial lobes each with very long basal collar and strong distal bristle; surstylus fused to epandrium; surstylus with apical setae as figured; cercus elongate, with 2 ventral mounds, the distal mound bearing setae; apical bladelike setae absent.

Female: similar to male.

Remarks: *Medetera longa* is here interpreted on the basis of 1 male and 2 females from Laos. Possible females are also known from the Philippines and the Malay Peninsula.

In describing the original Taiwanese specimens, Becker gave the male body length as 3.5 and that of the female as a much larger 4.5. The Laotian male and females however, are approximately the same length.

Medetera longa has unusually long legs and is distinguished by having the tibia longer than the femur on all three legs. Abdominal segment 7 is very long and is deeply cleft near its attachment with sternum 8.

Zoogeography

Distribution patterns. Widespread Oriental and Australasian species: *M. grisescens* has the most extensive range, from the western Indian Ocean to Hawaii, including south-eastern Asia to the Ryukyus and eastern Australia (Fig. 21). *Medetera austroapicalis* is also widespread, from the Indian subcontinent to the Solomon Islands, including south-eastern Asia to China and eastern Australia. These two species might be regarded as 'tramps', i.e., species of broad ecological tolerance, well adapted to survive in disturbed areas, and which are easily dispersed, perhaps even aided by human transport.

Oriental species: *M. platychira* (Fig. 22), *M. pumila, M. opaca, M. beckeri* and *M. vivida* are fairly widespread throughout the Oriental region, west of Weber's Line. The closely related species *M. bishopae* (Malaya, Borneo) and *M. chillcotti* (lowland Nepal) indicate a wide distribution for the *chillcotti* group. The four species of the *gracilis* group are confined to humid tropics of Malaysia, Indonesia and the Philippines. Three fairly closely related species are described from above 3000 m in Nepal: *M. nepalensis, M. himalayensis* and *M. stomias.* As well, ten species are known only from their respective type localities in Java, the Philippines, Borneo, Sri Lanka and Burma.

Indo-Australian species: *M. minima* ranges from Malaya to the Solomons, including Cape York Peninsula. The range of *M. olivacea* includes Indonesia, the Philippines and New Guinea (Fig. 23).

Australasian species: *M. salomonis,* an Australasian 'tramp', ranges from French Polynesia in the eastern Pacific through Samoa, Fiji, Melanesia, New Guinea, eastern and northern Australia, and the Philippines (Fig. 24). The other five Australasian

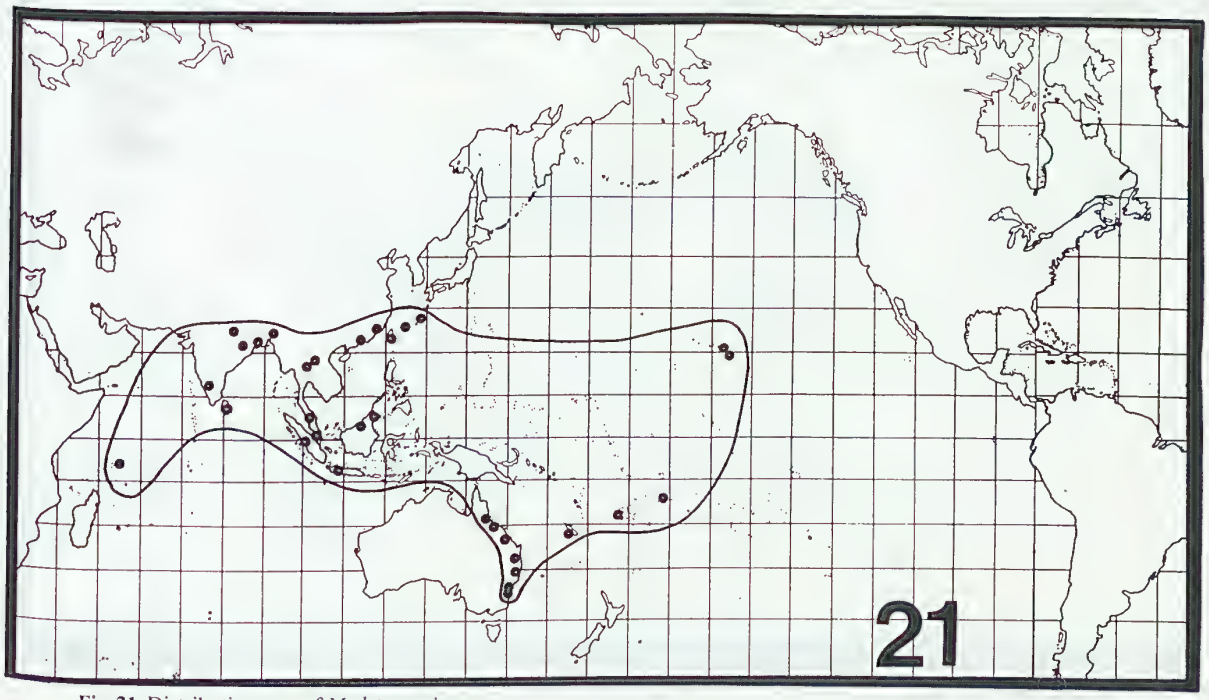

Fig. 21. Distribution map of *Medetera grisescens.*

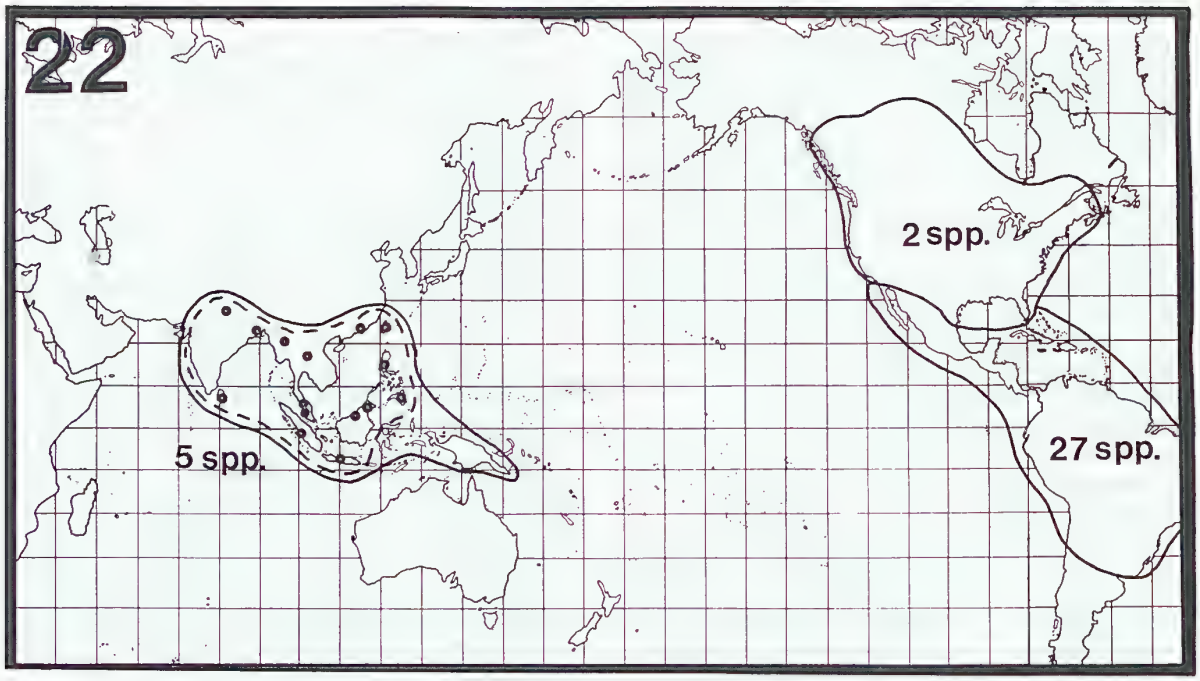

Fig. 22. Distribution map of *Medetera aberrans* species group:
● records of *M. platychira;* —distribution of *aberrans* species group with number of described species from each region.

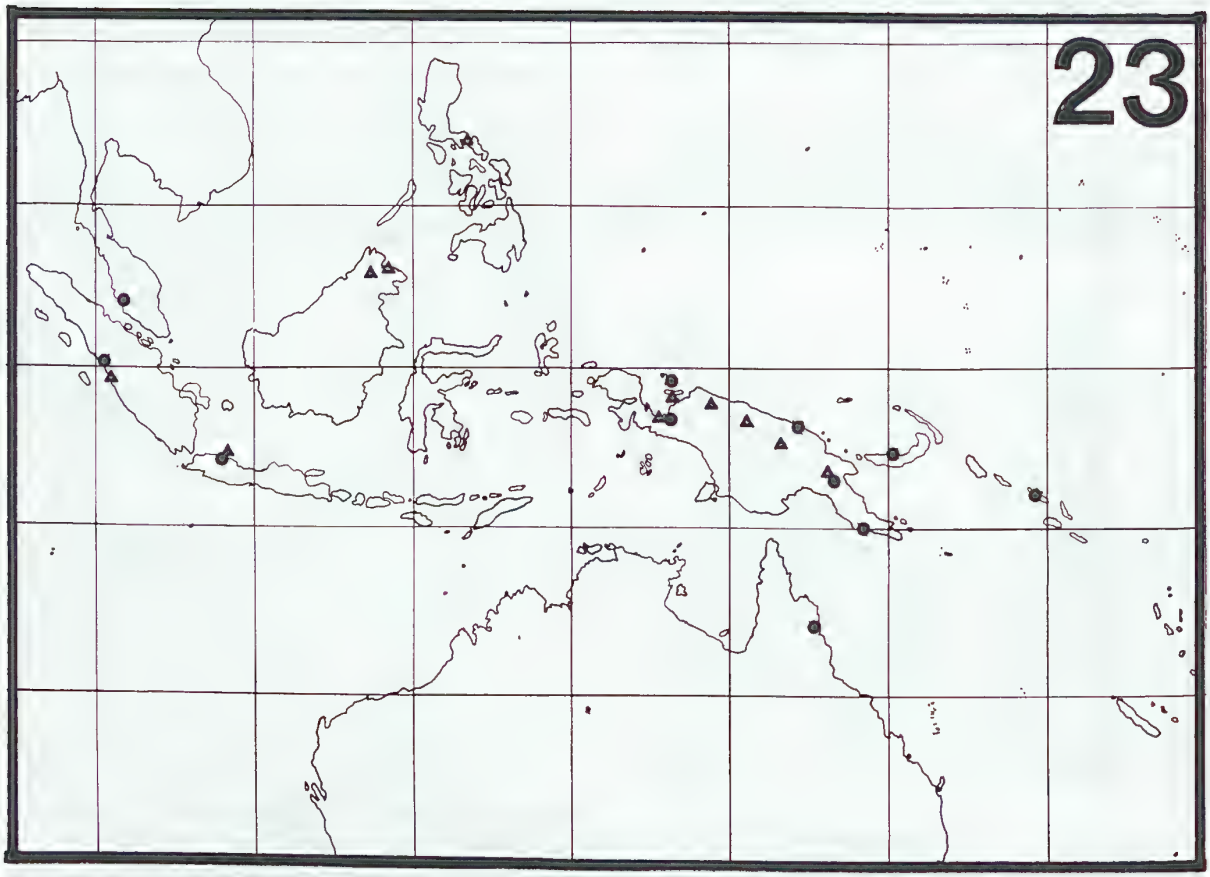

Fig. 23. Distribution map of *Medetera minima* and *Medetera olivacea:* ● *M. minima;* ▲ *M. olivacea*

members of the *salomonis* group are confined primarily to Melanesia and Australia. The *flaviscutellum* and *melanesiana* groups have distributions in New Guinea and eastern Australia, while the *toxopeusi* group is almost entirely confined to New Guinea. The *australiana* group is found only in eastern Australia, while *M. nigrohalterata* is found in both south-eastern and south-western Australia (Fig. 24). Within Australia, *Medetera* is most diverse in the coasts and ranges of Queensland and New South Wales, especially in tropical and subtropical closed forest. Only one species has a range which includes Victoria and Western Australia, and the genus is not recorded from Tasmania.

Pacific species: the patterns of distribution into the Pacific shows a classic 'sweepstake' dispersal pattern, with progressively fewer species towards the East (Fig. 25). In western 'source' areas such as New Guinea and the Philippines, both widespread and endemic species are present while in the eastern Pacific, there are no endemics and the fauna consists only of 'tramps.' *Medetera* has not been found in New Zealand, despite careful search by B. A. Holloway and subsequent personal examination of the NZAC. New Zealand is probably too far south to have received such good dispersalists as *M. grisescens* or *M. salomonis.*

Affinities and history. *Medetera* probably had its origin in the early Tertiary Northern Hemisphere mesophytic forests (Bickel, 1985). Evidence from the distribution and affinites of the Oriental and Australasian faunas does not contradict this hypothesis. Many Oriental and Australasian species either belong to diverse holarctic groups or can be derived from them. However, the Australasian region is an important secondary centre of diversity with several groups being almost entirely confined to New Guinea and eastern Australia. The absence of the genus from southern South America (Van Duzee, 1930) and New Zealand, and the impoverished fauna of southern Australia argue strongly against any Gondwanaland source area. Therefore, the following history of the Oriental and Australasian *Medetera* is suggested (with information from Matthews, 1979 and Keast, 1981).

Late Cretaceous-Early Tertiary: widespread circumboreal warm meosphytic forests were the centre of diversity in *Medetera.* During this time, broad zones of interchange were available between the northern continents and the genus was probably present throughout Laurasia including what is now southeastern Asia. Since the Australian Plate was positioned much further south and isolated, *Medetera* was undoubtedly absent from ancestral Melanesia-Australia.

Mid-Tertiary: cooling forced the southward retreat

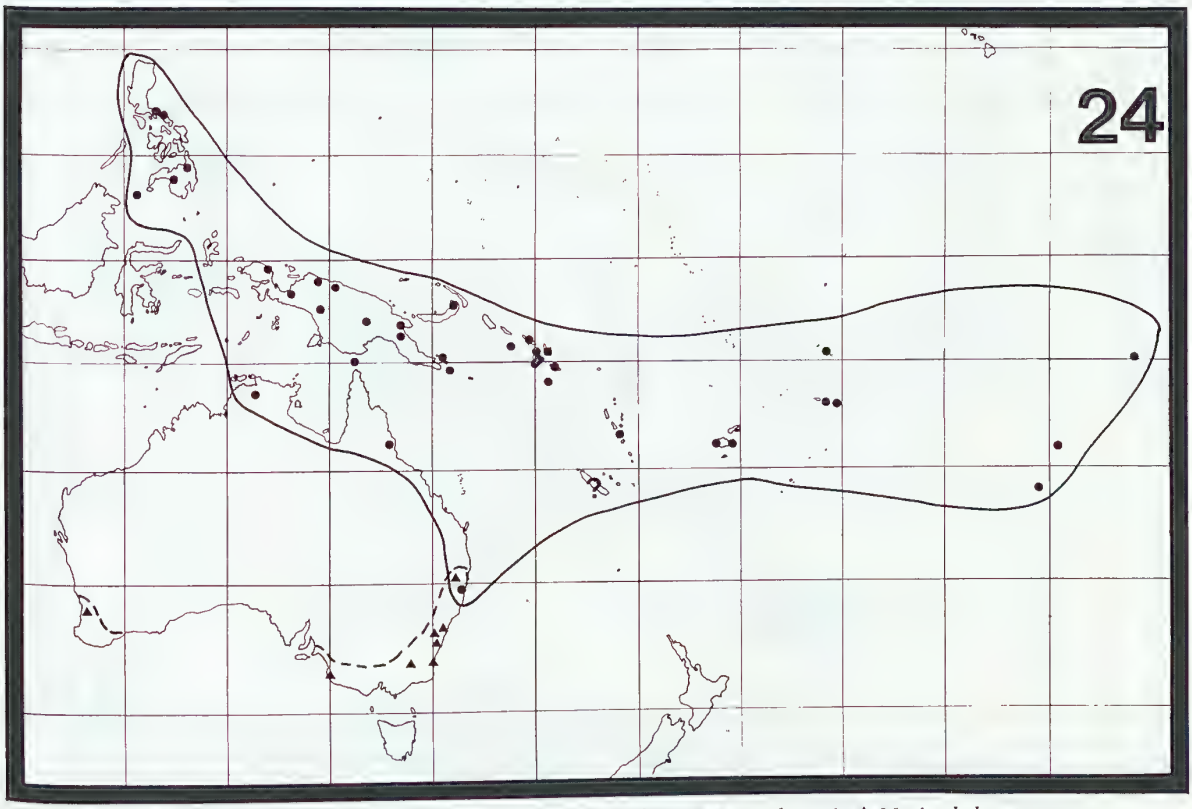

Fig. 24. Distribution map of *Medetera salomonis* and *M. nigrohalterata:* ● *M. salomonis;* ▲ *M. nigrohalterata.*

of circumboreal mesophytic forests and their associated insect faunas, splitting the *aberrans* group into disjunct or vicariant Old World and New World sections (Fig. 22). The Oriental *Medetera platychira,* is strikingly similar to the eastern nearctic *M. aberrans* (see figures in Bickel, 1985), indicating little morphological change since their separation. The palearctic genus *Dolichophorus* probably arose from the *aberrans* group at this time. As the Australian Plate moved closer to the Asian Plate, chance dispersal from the Oriental Region would have become increasingly probable, with sucessful dispersalists radiating on the Australian Plate, giving rise to the *melanesiana, salomonis, flaviscutellum, australiana* and *toxopeusi* groups.

Late Tertiary-Quaternary: as the Australian Plate moved closer to Asia, vulcanism and uplift along the Australian-Asian Plate boundaries caused formation of island arcs and diverse tropical montane habitats, thereby increasing faunal interchange (in both directions) and speciation. With increased aridity during the Miocene, the once continuous forests along the southern margin of Australia were split, resulting in disjunct populations of *M. nigrohalterata* in southeastern and south-western Australia. During the Quaternary, falling sea level would have facilitated dispersion between some island groups and across Torres Strait. Some 'tramp' species of successful holarctic groups, such as *M. grisescens* (*diadema-veles* group) and *M. australapicalis* (*apicalis* group) and a 'tramp' of Australasian origin, *M. salomonis,* probably increased their ranges during this time.

Medetera kinabaluensis, from high elevation (2140 m) on Mt Kinabalu, Sabah is a member of the predominately holarctic circumboreal *signaticornis-pinicola* group. This group contains many important predators of conifer-attacking scolytid beetles, and have been reared from various tree species, principally northern hemisphere conifers. In the New World, species extend southward into tropical Central American montane pine forests (Bickel, 1985). The presence of a member of the *signaticornis-pinicola* group in Borneo is of particular interest. Today, only two species of *Pinus* are found in the Malay Archipelago (Sumatra and the Philippines but not Borneo). However, pollen of three northern conifers, *Pinus, Picea* and *Tsuga,* is recorded from the Miocene of Brunei, but today these latter two genera are not found closer than 20°N on the Asian mainland (Whitmore, 1975). This coniferous flora maintained itself in Borneo until late Tertiary when it became extinct, possibly due to peneplanation of the old mountains. The major uplift of Mt Kinabalu was

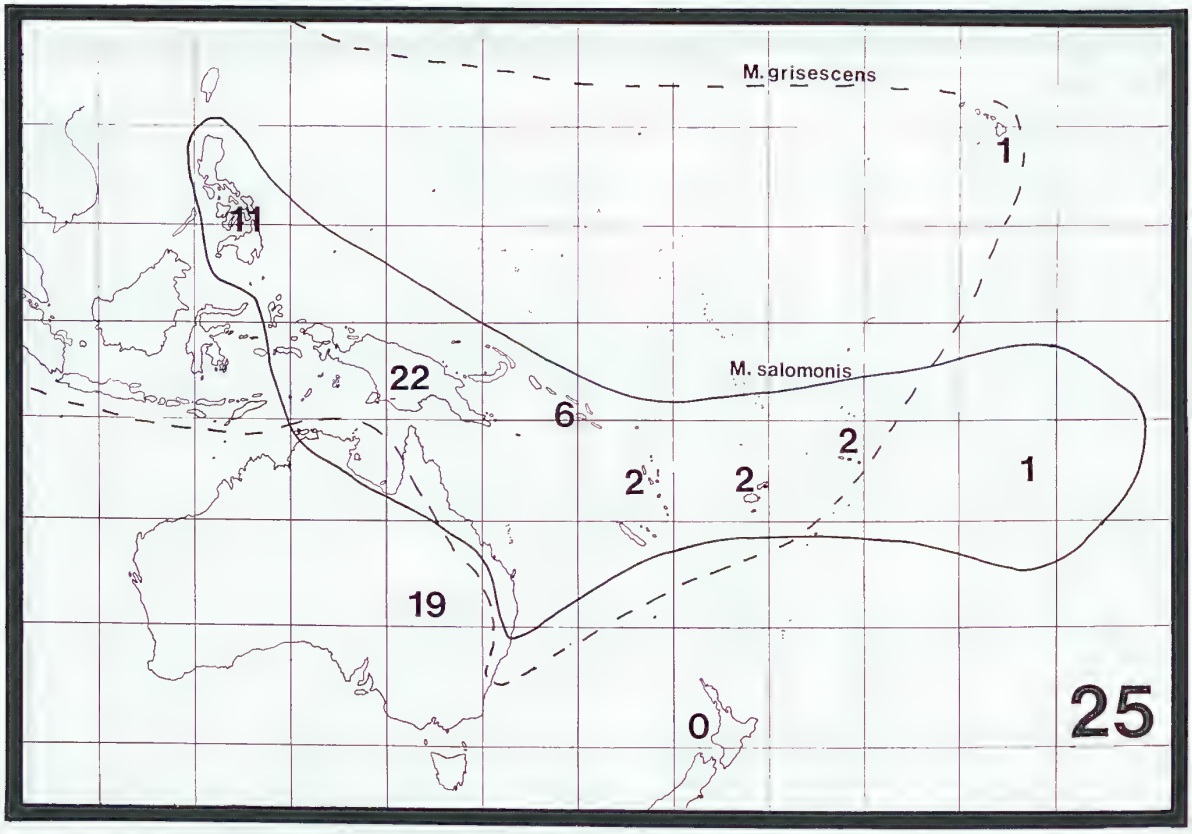

Fig. 25. Number of described Medetera species from Australasia and the Philippines. — *M. salomonis;* --- *M. griscens.*

relatively late, in the mid-Pleistocene, supposedly after the disappearance of the northern conifers (Holloway, 1970). At the 1000–2500 m zone on Mt Kinabalu, the vegetation is dominated by lauro-fagaceous forest of south-east Asian and Himalayan foothills affinities, while at higher elevations, a mixture of south temperate and Himalayan plants predominates. Holloway's analysis of the Mt Kinabalu moth fauna showed that palearctic elements are present only at high altitudes and that these elements have related species on high peaks in Luzon and Sumatra. Since Mt Kinabalu is a young peak, Holloway assumed that palearctic elements must have colonized the mountain relatively recently, since the beginning of the Pleistocene, from a northern source area. However, some of these palearctic elements may not be recent immigrants at all, but remnants of early Tertiary stock originally associated with the 'northern' coniferous flora but which became secondarily associated with the present montane forests. The strong association of the *signaticornis-pinicola* group with conifers would support this latter hypothesis, and *Medetera kinabaluensis*, of holarctic affinities, may in fact be a very old member of the Bornean fauna.

Phylogenetic Analysis

I presented (Bickel, 1985) a cladistic analysis of the Medeterinae in which the genus *Thrypticus* was regarded as derived from *Medetera*. This analysis was modified in Bickel, 1986, and *Thrypticus* + *Corindia* is now regarded as the sister-group of *Medetera*. The following analysis considers the phylogenetic relationships of the major holarctic, Oriental and Australasian *Medetera* groups.

Most characters and their character states were discussed in Bickel (1985, 1986) and will be summarized in the following format: Character: plesiomorphic (ancestral) state/ apomorphic (derived) state.

1. Vestiture of eyes: short hairs present/ bare.
2. Proboscis: weakly sclerotized/ massive, heavily sclerotized.
3. Postsutural supraalar bristles (sa): 2/ 1, the anterior bristle lost.
4. Lateral scutellars: strong bristles/ reduced to short hairs or lost.
5. Acrostichals: present/ reduced in size or lost
6. Thorax: of normal shape/ thorax prolonged with increased separation of coxae I and II.
7. Thorax: unicolourous metallic/ scutellum, posterior mesonotum, and postpronotum yellowish, contrasting with the generally darker metallic thoracic colouration; found in the *toxopeusi*, *flaviscutellum* and *gracilis* species groups.
8. Orientated silvery pruinosity in patches on thorax, legs, and abdomen: absent/ present in the *gracilis* group.

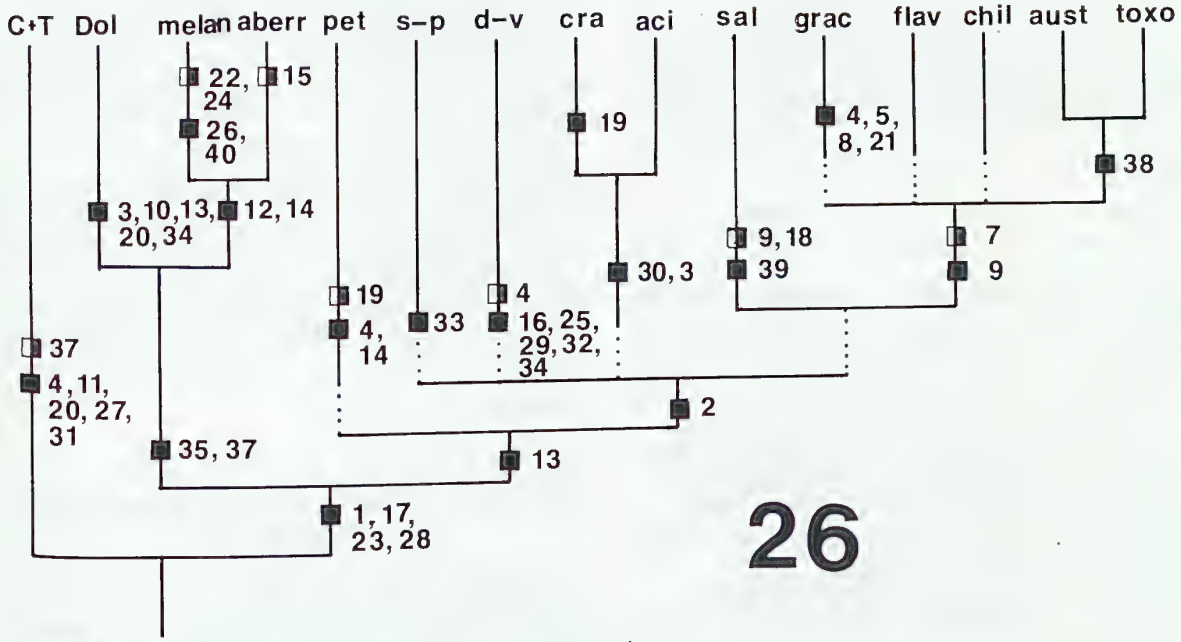

Fig. 26. Cladogram of Holarctic, Oriental and Australasian *Medetera*
■ Apomorphy □ Apomorphy shared by only some members of group.
Abbreviations: aberr, *aberrans* group; aci, *apicalis* group; aust, *australiana* group; chil, *chillcotti* group; cra, *crassivenis* group; d-v, *diadema-veles* group; flav, *flaviscutellum* group; grac, *gracilis* group; melan, *melanesiana* group; sal, *salomonis* group; s-p, *signaticornis-pinicola* group; toxo, *toxopeusi* group; C+T, *Corindia* + *Thrypticus;* Dol, *Dolichophorus.*

9. Dorsocentrals (dc): 3–5 present, decreasing in size anteriorly/ only 2 strong dc bordering mesoscutal depression, anteriors as short setulae.
10. Strong anterolateral bristle on coxa I: absent/ present.
11. Coxa III lateral bristles: 1/ 2.
12. Femora II and III: with normal vestiture/ with strong anterior setae.
13. Femur II posterior subapical bristle: present/ absent.
14. Male tibia III: unmodified/ with anteroapical spur (MSSC).
15. Male tarsus I: unmodified/ tarsomeres 2–3 flattened, modified.
16. Male basitarsus III: unmodified/ with anteroventral basal tooth (MSSC).
17. Distal sectors of veins M and R_{4+5}: straight, subparallel to apex/ arched anteriorly, somewhat converging.
18. Distal vein M: arched anteriorly/ arched or bowed posteriorly.
19. Male basal CuA: unmodified/ thickened
20. Anal vein: present/ reduced or lost.
21. Anal angle of wing: present/ lost (Fig. 2e) in the *gracilis* group.
22. Male postabdomen: strongly sclerotized and metallic coloured/ weakly sclerotized and unmelanized distal half of segment 6, all of segments 7 and 8 and basal portion of epandrium found in some species of the *melanesiana* group.
23. Position of the hypopygial foramen: left basolateral/ left mid-dorsolateral.
24. Position of the hypopygial foramen: left middorsolateral/ secondary migration to basal position in some species in the *melanesiana* group.
25. Epandrium (lateral view): subrectangular/ pyriform.
26. Epandrium: cylindrical/ dorsoventrally flattened.
27. Flexion of hypandrium: absent/ present.
28. Hypandrium, attachment to epandrium: basal/ midventral.
29. Hypandrium: broad, rectangular/ narrow, tapering.
30. Hypandrium: flat over aedeagus /'clasping' aedeagus.
31. Apex of aedeagus: simple/ cleft, or notched.
32. Epandrial seta: present/ reduced or lost.
33. Epandrial lobe bases: short, collar-like/ long, cylindrical, and positioned laterad of each other.
34. Epandrial lobes: bases separate/ bases fused.
35. Relative length of ventral and dorsal surstylar arms: subequal/ dorsal arm longer.
36. Frayed ventral surstylar seta: absent/ present.
37. Cercus: undifferentiated/ with strong projecting distolateral arm.
38. Aedeagus: bent at right angle upon entering epandrium/ strongly recurved within epandrium.
39. Cercus: undivided/ secondarily segmented, with freely articulated basal and distal sections, as found in the *salomonis* group.
40. Cerci: free/ fused medially.

A cladogram representing the relationships of *Corindia, Thrypticus, Dolichophorus* and the major *Medetera* species groups is presented in Fig. 26. The relationship of *Corindia* + *Thrypticus* with *Medetera* was discussed by Bickel, 1986a.

Medetera is defined by strong apomorphies 1, 17, 23 and 28. *Dolichophorus,* a palearctic genus of two species, is defined by autapomorphies 3, 10, 13, 20 and 34 and is considered the sister taxon of the *aberrans* + *melanesiana* groups. Recognition of *Dolichophorus* as a separate genus makes *Medetera* paraphyletic, since it does not include all of its descendant groups. However, *Dolichophorus* is clearly defined, and to submerge this genus within *Medetera* would only serve to dilute the concept of *Medetera.* Perhaps the lineage including *Dolichophorus* and the *aberrans* + *melanesiana* groups should be split off as a separate genus, making it the sister group to *Medetera* s.s. However, I will not alter the current concepts of these two genera, and will let *Medetera* stand as a paraphyletic taxon until an analysis of the world Medeterinae is completed.

The monophyly of the *aberrans* + *melanesiana* complex is strongly supported by synapomorphies 12 and 14. The *melanesiana* group is an Australasian offshoot of the widespread *aberrans* group and is defined by autapomorphies 26 and 40.

Medetera s.s is rather weakly defined by apomorphy 13, the loss of the FII posterior subapical bristle, which is homoplastic with *Dolichophorus.* Although the holarctic *petulca* group, the *signaticornis-pinicola* group, the *diadema-veles* group and the *apicalis* + *crassivenis* complex are each fairly well defined by autapomorphies, no strong synapomorphies can be found to link them.

The *gracilis, flaviscutellum, chillcotti, australiana* and *toxopeusi* groups all are linked by a moderately strong synapomorphy 9, reduction of dorsocentrals to 2 strong dc bordering the mesoscutal depression. The *australiana* and *toxopeusi* groups share strong synapomorphy 38, the internally recurved aedeagus. The *salomonis* group is strongly defined by autapomorphy 39 and is possibly linked to the five groups considered above.

Additional Oriental Records and Nomenclatorial Notes

In eastern Asia the boundary between the Oriental and palearctic zoogeographical regions is arbitrarily defined. Since no significant physiographic feature acts as a biotic barrier, mixing of elements from the two regions must be expected.

The Ryukyu Islands form part of the northern boundary of the Oriental region. In addition to *M. grisescens,* recorded above, the following holarctic

and palearctic species (see Negrobov, 1971–77, and Bickel, 1985) are present on these islands (BPBM).

Medetera apicalis, 5♂♂, 7♀♀, Amami-Oshima Island, Mt Yuwan-dake, 550 m, 17 July 1963; Iromuk Island, 100 m, 11–12 March 1964.

M. veles, 2♂♂, 2♀♀, Ishigaki Island, Kora-yama, 14–18 March 1964.

Close to *M. jacula* (possibly the closely related *M. flavipes*), 6♂♂, 24♀♀, Ishigaki Island, Kora-yama, 14–18 March 1964.

Medetera adsumpta Becker (1922: 48) and *M. nudicoxa* Becker (1922: 52) were described from India. I have been unable to see the type material (Zoological Survey of India, Calcutta) and therefore have not included the two species in this revision. However, based on Becker's descriptions, *M. adsumpta* is possibly a member of the *chillcotti* group while *M. nudicoxa* is almost certainly in the *apicalis* group and close to *M. himalayensis-M. nepalensis*.

The types of *Medetera comes* Hardy (1939: 352), from Brisbane, are lost. From Hardy's brief description it is possible that this species is a member of the *australiana* group. *Medetera comes* is regarded as a *nomen dubium*.

The types of *M. extranea* Becker (1922: 49) described from Sydney and deposited at the Hungarian National Museum, Budapest, have been lost. The species Becker described is very small, 1.0–1.2 mm long, has veins R_{4+5} and M running parallel to the apex, white or pale body setae, and black antenna. I have seen no *Medetera* species which matches this description. If the scape and pedicel were yellow, this description would serve for one of the small species in the medeterine genus *Corindia*. Possibly this species belongs in another subfamily. *Medetera extranea* is therefore regarded as a *nomen dubium*.

I have examined the two male syntypes of *Medetera vegandris* Frey (1925: 24) described from the Philippines (ZMH, Type No. 14020). This species does not belong in *Medetera*. From its small size, wing venation, lack of acrostichals, and male postabdominal structure, it belongs to the genus *Micromorphus*. Therefore, *Medetera vegandris* is regarded as *Micromorphus vegandris* (Frey), new combination.

ACKNOWLEDGEMENTS. I would like to thank the following institutions and their respective curators for the loan of specimens. Any reference to these institutions will use the abbreviations designated below:

AMNH American Museum of Natural History, New York; P. Wygodzinsky, R. Shuh.
AMS Australian Museum, Sydney; D.K. McAlpine.
ANIC Australian National Insect Collection, CSIRO, Canberra; D.H. Colless, Z. Liepa.
BMNH British Museum (Natural History), London; K. G. V. Smith.
BPBM Bernice P. Bishop Museum, Honolulu; W. A. Steffan, N. Evenhuis.
CED C.E. Dyte personal collection, Slough, U.K.
CNC Biosystematics Research Institiute, Agriculture Canada, Ottawa; J. R. Vockeroth.
CUIC Cornell University, Ithaca, New York; L. L. Pechuman.
DEI Institut für Pflanzenschutzforshung der Akademie der Landwirtschaftswissenschaften der DDR, Eberswalde-Finow, Germany (formerly Deutsches Entomologisches Institut); G. Morge.
MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; A. F. Newton.
MVM Museum of Victoria, Melbourne; A. Neboiss.
NZAC New Zealand Arthropod Collection, DSIR, Auckland; B. Holloway.
PDPI Papua New Guinea Department of Primary Industries, Konedobu; J. Ismay.
QDPI Queensland Department of Primary Industries, Brisbane; B. Cantrell.
QMB Queensland Museum, Brisbane; E. C. Dahms.
SAM South Australian Museum, Adelaide; L. Queale.
UQIC University of Queensland Insect Collection, Brisbane; M. Schneider.
USNM National Museum of Natural History, Smithsonian Institution, Washington, D.C.; F.C. Thompson.
ZMH Zoologiska Museum, Helsinki, Finland; B. Lindeberg.
ZMHB Zoologisches Museum, Humboldt Universitat, Berlin; H. Schumann.
ZMUA Zoologisch Museum, Universiteit van Amsterdam, Netherlands; T. van Leeuwen, P. Oosterbroeck.
ZUMC Zoologisch Museum, Universitets Copenhagen, Denmark; L. Lyneborg, V. Michelsen.

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References

Becker, T., 1917. Dipterologische Studien. Dolichopodidae. Nova Acta Academiae Caesareae Leopoldino Carolinae 102: 113–361.

———— 1922. Dipterologische Studien, Dolichopodidae der indo-australischen Region. Capita Zoologica 1x:1–247.

Bickel, D.J., 1985. A revision of the Nearctic *Medetera* (Diptera: Dolichopodidae). United States Department of Agriculture Technical Bulletin 1692: 1–109.

———— 1986. *Thrypticus* and an allied new genus, *Corindia* from Australia (Diptera: Dolichopodidae). Records of the Australian Museum 38: 135–151.

———— 1986b. *Atlatlia*, a new genus from Australia (Diptera: Dolichopodidae). Entomologica Scandinavica 17: 165–171.

———— 1986c. Australian *Systenus* (Diptera: Dolichopodidae). Records of the Australian Museum 38(5): 263–270.

Dyte, C.E., 1975. Family Dolichopodidae in 'A Catalog of

the Diptera of the Oriental Region' Vol. 2: 212–260 (M.D. Delfinado & D.E. Hardy, eds). University Press of Hawaii, Honolulu.

Fischer von Waldheim, G., 1819. Programme d'invitation à la séance publique de la Société Impérial des Naturalistes, qui aura lieu le 15 Decembre, contenant une notice d'une mouche carnivore. Moscou, 11 pp.

Frey, R., 1925. Philippinische Dipteren II. Fam. Dolichopodidae. Notulae Entomologicae 5: 15–27.

Keast, A., ed. 1981. Ecological biogeography in Australia. 3 vols. W. Junk, The Hague.

Hardy, D.E. & M.A. Kohn, 1964. Dolichopodidae, vol 11: 1–256. **In** 'Insects of Hawaii' (E.C. Zimmerman, ed.). University of Hawaii Press, Honolulu.

Hardy, G.H., 1939. Miscellaneous notes on Australian Diptera. VI. Proceedings of the Linnean Society of New South Wales 64: 345–352.

Hollis, D., 1964. Notes and descriptions of Indonesian Dolichopodidae (Insecta, Diptera) in the Zoologisch Museum, Amsterdam. Beaufortia 10: 239–274.

Holloway, J.D., 1970. The biogeographical analysis of a transect sample of the moth fauna of Mt. Kinabalu, Sabah, using numerical methods. Biological Journal of the Linnean Society 2: 259–286.

McAlpine, J.F., 1981. Morphology and Terminology – Adults, pp. 9–64 **in** 'Manual of Nearctic Diptera' J.F. McAlpine, et al., Vol. 1, Research Branch Agriculture Canada, Monograph 27, Ottawa, 674 pp.

Mani, M.S., 1968. Ecology and biogeography of high altitudes. Series Entomologica, Vol. 4. W. Junk, The Hague, 527pp.

Matthews, J.V., 1979. Tertiary and Quaternary environments: historical background for an analysis of the Canadian insect fauna. Pp. 31–82 **in** 'Canada and its Insect Fauna' (Danks, H.V., ed.). Memoirs of the Entomological Society of Canada 108: 1–573.

Meijere, J. C. H. de, 1916. Studien über südostasiatische Dipteren. XII. Javanische Dolichopodiden und Ephydriden. Tijdschrift voor Entomologie 59: 225–273.

Negrobov, O.P., 1971–1977. Dolichopodidae, Unterfamilie Medeterinae. **In** 'Die Fliegen der palaearktischen Region' (E. Lindner, ed.) 29: 269–353, Lieferungen 284 (1971), 289 (1972), 302 (1974), 303 (1974), 316 (1977). Schweizerbart, Stuttgart.

Negrobov, O.P. & E. Thuneberg, 1970. Some questions on the systematics of the genus *Medetera* (Dipt., Dolichopodidae) of the Palearctic region. Annales Entomologici Fennici 36: 143–145.

Parent, O., 1932a. Contribution à la Faune Diptérologique (Dolichopodidae) d'Australie-Tasmanie. Annales de la Société scientifique de Bruxelles (B)(Mémoirs) 52: 105–176.

_____ 1932b. Fauna Buruana, Diptera, Dolichopodidae. Treubia 7(Suppl.): 349–353.

_____ 1935. Diptères Dolichopodides conservés au Muséum des États Malais Confédérés. Annals and Magazine of Natural History (10) 15: 194–215.

_____ 1941. Diptères Dolichopodides de la région, Indoaustralienne. Espèces et localités nouvelles. Annals and Magazine of Natural History (11)7: 195–235.

Robinson, H., 1970. Family Dolichopodidae. **In** 'A Catalogue of the Diptera of the Americas south of the United States' (N. Papavero, ed.). Part 40: 1–92. Museu de Zoologia, Universidade São Paulo, Brasil.

Steyskal, G.C., 1967. Replacement names for preoccupied specific names in Dolichopodidae (Diptera). Proceedings of the Entomological Society of Washington 69: 224.

Van Duzee, M.C., 1925. New species of North American Dolichopodidae (Diptera). Psyche 32: 178–189.

_____ 1933. New Dolichopodidae from the Hawaiian Islands (Diptera). Proceedings of the Hawaiian Entomological Society 8: 307–357.

_____ Dolichopodidae. Part 5(1) **in** 'Diptera of Patagonia and South Chile'. British Museum (Natural History), London.

Whitmore, T.C., 1975. Tropical rain forests of the Far East. Oxford University Press, London, 282 pp.

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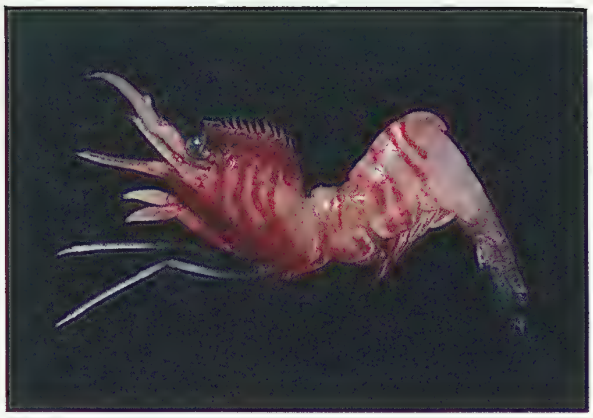

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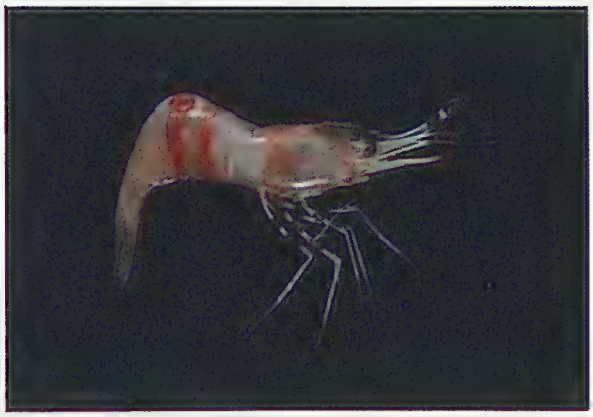

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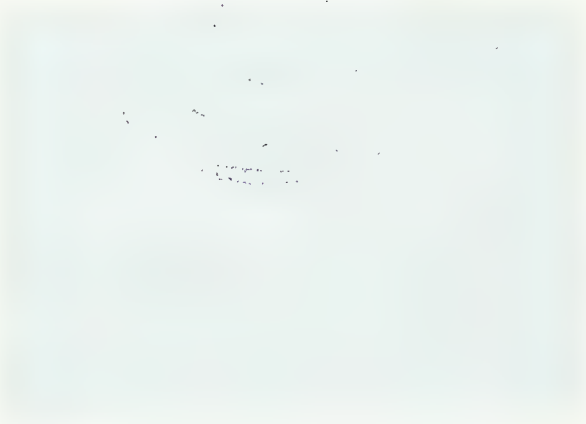

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Deepwater Decapod Crustacea from Eastern Australia (Penaeidea and Caridea)

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ABSTRACT. A taxonomic report on deepwater shrimps and prawns from Eastern Australia, primarily New South Wales, is presented. The collection, which includes penaeideans and carideans, consists of 73 species. Of these, 46 represent new records for the Australian fauna, while ten species and one subspecies are described as new. These latter are: *Haliporoides cristatus, H. sibogae australiensis, Pasiphaea berentsae, P. kapala, P. longitaenia, Lebbeus yaldwyni, Merhippolyte chacei, Plesionika grahami, Glyphocrangon holthuisi, G. lowryi* and *G. novacastellum.* Locality data and diagnoses are provided for all the species. Zoogeographically, the collection is made up of two major components: those species having a widespread distribution in all the oceans, and those which are Indo-Pacific in distribution.

KENSLEY, B., H.A. TRANTER & D.J.G. GRIFFIN, 1987. Deepwater decapod Crustacea from eastern Australia (Penaeidea and Caridea). Records of the Australian Museum 39(5): 263–331.

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The deepwater shrimps and prawns of eastern Australia are at present known only from early work by the *Challenger* (Bate, 1888) and the *Endeavour* (Schmitt, 1926) expeditions. Most of the studies since that time have concerned the commercially important penaeideans and few of these studies have dealt with deepwater species. Griffiths & Brandt (1983) briefly summarised the distribution of some mesopelagic species. Racek & Dall, in a series of major papers, have dealt with the shallow water penaeideans of Australia. Published work on penaeidean and caridean decapod crustaceans from other geographic areas form a sound basis for studies of the local fauna. These include the works of Calman (1925, 1939), Chace, in a series of extremely significant papers (1940, 1983, 1984, 1985), Crosnier (1970, 1976, 1978, 1985), Crosnier & Forest (1973), Hayashi & Miyake (1969), Holthuis (1951, 1955), Kensley (1968, 1971, 1977, 1981), Kubo (1949), Pérez Farfante (1977), and Yaldwyn (1960, 1967).

Since 1971, the New South Wales State Fisheries (now the Fisheries Division of the NSW Department of Agriculture) has been carrying out a series of trawling surveys along the coast of New South Wales, extending into Queensland waters to the north and the Bass Strait to the south, with a view to understanding the distribution of prawns (see Australian Fisheries, November 1973, pp. 24–29). Well over 100 species of crabs, lobsters, and shrimps have been found as a result of these studies. Of these, more than 40 have been recognised in the last ten years.

The present paper is a report on the shrimps and prawns collected between 1971 and 1984. Seventy three species are recorded here. The sergestid shrimps have not been dealt with, as these will form part of a separate study, along with the sergestid fauna of New Zealand. There are at least 13 species of sergestids in the NSW collection. One new species from this collection, *Cryptopenaeus crosnieri* Pérez Farfante & Kensley, 1985, was described in a separate paper.

The material on which this paper is based is deposited in the collections of the Australian Museum (AM); some paratypic material has been deposited in the Smithsonian Institution. Each species account includes the original reference to the species, and either references to all Australian literature relevant to that species, or to a recent adequate Australian treatment of the species. Also included is a list of material examined along with locality data, a remarks section where necessary, and a summary of the geographic and bathymetric distribution. Carapace length (cl) is used as the standard measurement. Within each family, genera and species are arranged alphabetically.

SYSTEMATIC SECTION

Infraorder PENAEIDEA

Family SOLENOCERIDAE

Haliporoides Stebbing, 1914

***Haliporoides cristatus* n. sp.**

Figs 1, 2, 5G–L

Haliporoides sp.—Potter & Dredge, 1985: 226.

Type material. New South Wales: HOLOTYPE: AM P35893, north-east of Point Danger, 27°55′S 154°03′E to

27°57′S 154°03′E, 629 m, demersal prawn trawl, *Kapala* (K78-23-09), 6 Nov 1978; 1 ♂, 23.5 mm. PARATYPES: AM P35894, east of Broken Bay, 33°43–39′S 151°54–55′E, 477 m, demersal prawn trawl, *Kapala* (K83-14-07), 27 Oct 1983; 1 ♂ (juv.) 16.0 mm, 8 ♀, 16.8–22.6 mm. AM P21588, north-east of Point Danger, 28°01′S 154°00′E to 27°58′S 154°00′E, 542 m, demersal prawn trawl, *Kapala* (K78-17-10), 17 Aug 1978; 1 ♂, 21.0 mm. AM P21699, south-east of Cape Hawke, 32°22′S 152°58′E to 32°17′S 153°01′E, 463 m, demersal prawn trawl, *Kapala* (K75-08-03), 2 Oct 1975; 1 ♂, 17.0 mm. USNM 211386, south-east of Broken Bay, 33°40′S 151°54′E to 33°33′S 151°58′E, 250 m, demersal prawn trawl, *Kapala* (K74-15-25/26), 5 Dec 1974, 1 ♂, 18.8 mm, 4 ♀, 17.5–23.2 mm. USNM 211387, east of Broken Bay, 33°43–39′S 151°54–55′E, 477 m, demersal prawn trawl, *Kapala* (K83-14-07), 27 Oct 1983, 1 ♂, 20.5 mm, 4 ♀, 21.0–22.9 mm.

Additional material examined. New South Wales: AM P33171, north-east of Point Danger, 28°01′S 154°00′E to 27°58′S 154°00′E, 542 m, demersal prawn trawl, *Kapala* (K78-17-10), 17 Aug 1978; 8 ♀. AM P21585, north-east of Sydney, 33°43′S 151°49′E, 411 m, *Kapala,* 28 Sept 1975; 4 ♂, 3 ♀. AM P21767, north-east of Yamba, 29°26′S 153°49′E to 29°20′S 153°50′E, 450 m, demersal prawn trawl, *Kapala* (K75-09-08), 12 Oct 1975; 1 ♀. AM P24805, north-east of Batemans Bay, 35°28′S 150°50′E to 35°33′S 150°47′E, 594 m, demersal fish trawl, *Kapala* (K76-11-12), 8 July 1976; 5 ♀. AM P25064, east of Broken Bay, 33°34′S 152°08′E, 457 m, *Kapala,* 1 Nov 1976; 1 ♂, 2 ♀. AM P25206, south-east of Broken Bay, 33°42′S 151°52′E to 33°39′S 151°54′E, 446 m, demersal prawn trawl, *Kapala* (K76-24-01), 20 Dec 1976; 6 ♂, 1 ♀. AM P26819, south-east of Newcastle, 32°59′S 152°34′E to 33°02′S 152°31′E, 360 m, demersal prawn trawl, *Kapala* (K77-23-08), 7 Dec 1977; 1 ♂, 2 ♀. AM P33167, north-east of Port Jackson, 33°46′S 151°49′E to 33°44′S 151°51′E, 425 m, demersal prawn trawl, *Kapala* (K80-21-04), 16 Dec 1980; 1 ♂, 1 ♀. AM P35919, off Sydney, 33°46′S 151°50′E to 33°42′S 151°53′E, 414 m, demersal prawn trawl, *Kapala* (K80-06-01), 24 May 1980; 2 ♂, 1 ♀. AM P33170, north-east of Point Danger, 27°55′S 154°03′E to 27°57′S 154°03′E, 629 m, demersal prawn trawl, *Kapala* (K78-23-09), 6 Nov 1978; 4 ♂, 5 ♀. AM P33172, south-east to east of Broken Bay, 33°43′S 151°52′E to 33°40′S 151°55′E, 405 m, demersal prawn trawl, *Kapala* (K77-12-01/02), 8 Aug 1977; 3 ♂, 1 ♀. AM P33168, north-east of Wollongong, 34°21′S 151°25′E to 34°19′S 151°27′E, 432 m, demersal prawn trawl, *Kapala* (K78-27-13), 13 Dec 1978; 2 ♀. Queensland: AM P25146, east of Fraser Island, 366 m, *Markwell Enterprise;* 9 ♀.

Description. Integument firm, with overall fine pile of very short setae. Rostrum just reaching base of antennular peduncle article 3, strongly arched over eye, uniform in height from orbital margin to first ventral tooth, then tapering abruptly to apex. Rostral and epigastric teeth: $\frac{8+1}{2}$ to $\frac{11+1}{4}$; most frequent: $\frac{10+1}{3}$; epigastric tooth situated about ⅓ carapace length from orbital margin; first rostral tooth situated just posterior of orbital margin. Adrostral carina strong, acute, running from orbital margin to base of rostral apex. Postrostral carina barely marked, obsolete at level of cervical groove. Pterygostomian spine strong, triangular, lacking distinct keel, but basally rounded and extending into rounded hepatic carina. Hepatic sulcus deep. Cervical carina strong, rounded ventrally, obsolete at mid-dorsum. Suprahepatic spine subequal to hepatic spine. Posthepatic carina obsolete. Branchiocardiac carina rounded, sulcus relatively deep, not reaching posterior carapace margin. Postorbital spine subequal in strength to hepatic and suprahepatic spines. Submarginal carina acute, not quite reaching posterior margin of carapace.

Eye as illustrated.

Antennular peduncle about 0.6X length of carapace; prosartema not quite reaching distal margin of cornea; stylocerite short, basally broad, spine acute, falling considerably short of base of antennular peduncle article 2. Inner antennular flagellum 7X carapace length, outer flagellum 5X carapace length. Scaphocerite over-reaching antennular peduncle by about ⅛ of its own length, strongly rigid lateral margin ending in acute spine, falling short of apex of lamella; flagellum about 9X carapace length.

Mouthparts as figured.

Mandibular palp, second article almost 3X longer than wide, widest proximally; distal article about ⅔ length of proximal, slender, tapering, apically rounded. Maxilliped 3 extending beyond antennular peduncle by dactylus and half of propodus; dactylus slightly more slender and tapering in female than in male. Pereopod 1 reaching just beyond carpocerite in male and female; merus with distoventral movable spine and 3 fixed proximal spines; basis and ischium with distoventral fixed spine. Pereopod 2 reaching to base of antennular peduncle article 3 in female; almost to distal end of antennular peduncle article 2 in male. Pereopod 3 reaching by length of dactylus and propodus beyond antennular peduncle in female; by length of dactylus and half of propodus in male. Coxal plate of pereopod 3 in female expanded mesially, anterior surface hollowed, posterior surface strongly convex. Pereopod 4 extending beyond antennular peduncle by length of dactylus and ¾ length of propodus in female. Pereopod 5 extending beyond antennular peduncle by length of dactylus, propodus and carpus in female. Pereopods increasing in length posteriorly; anteromesial spine on coxae of pereopods 3–5 in both sexes; in female, coxal spine on pereopod 4 largest; in male, coxal spines of pereopods 3 and 4 small, on 5, spine becomes broad, flattened, distally rounded, directed ventrolaterally. Abdomen with segments 4–6 mid-dorsally sharply keeled, ending posteriorly in very small spine. Abdominal segment 6 only slightly longer than broad, ventral margin evenly convex, with single small denticle (sometimes absent) posteriorly. Telson with median sulcus deepest in anterior half, flattening out posteriorly,

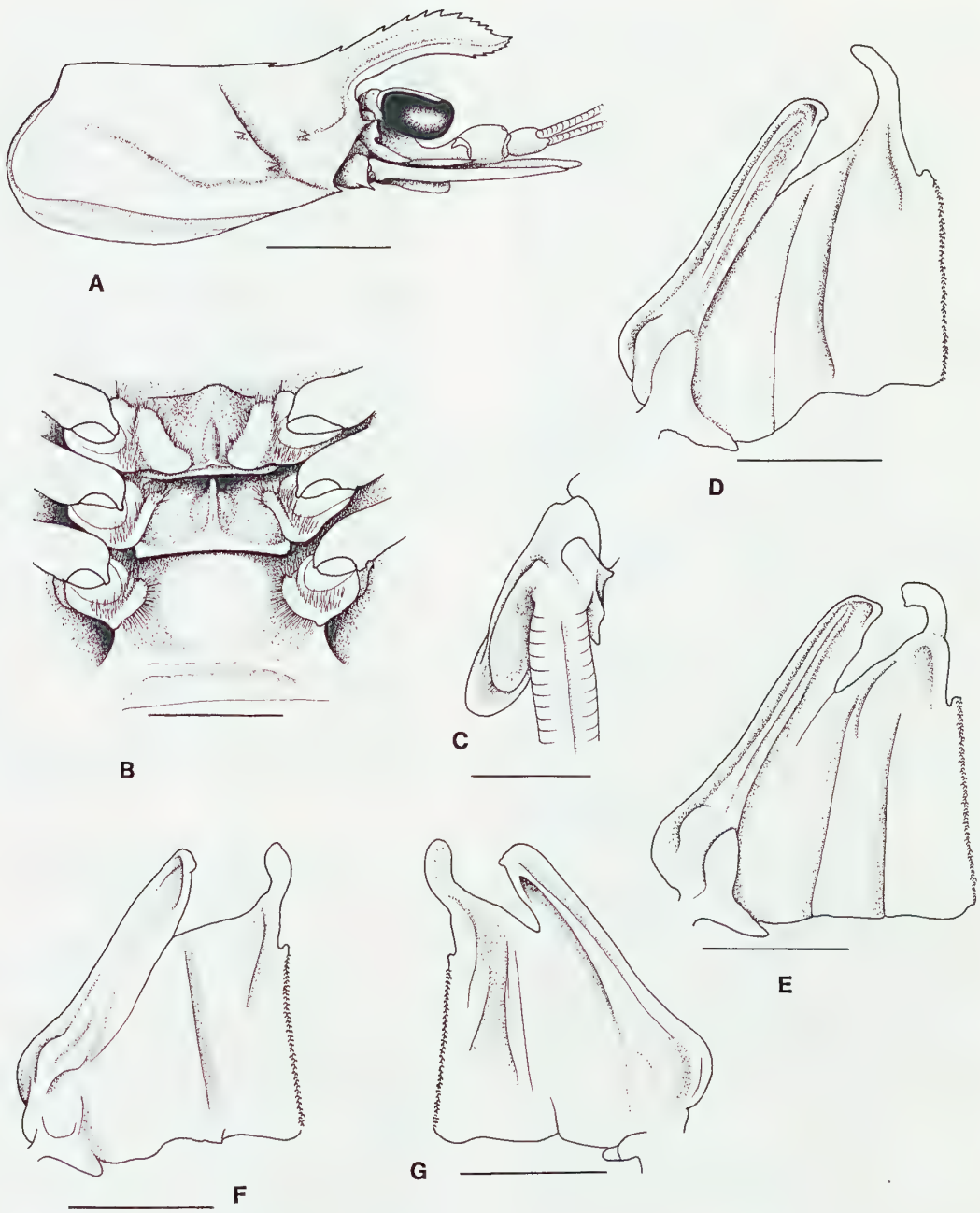

Fig. 1. *Haliporoides cristatus* n. sp. **A,** carapace in lateral view; **B,** thelycum; **C,** pleopod 2 ♂, appendix masculina. Petasmata: **D,** cl 22.9 mm; **E,** cl 24.5 mm; **F,** cl 31.5 mm; **G,** cl 21.8 mm. (Scales: A = 10 mm, B = 5 mm, C = 2 mm, D-G = 3 mm).

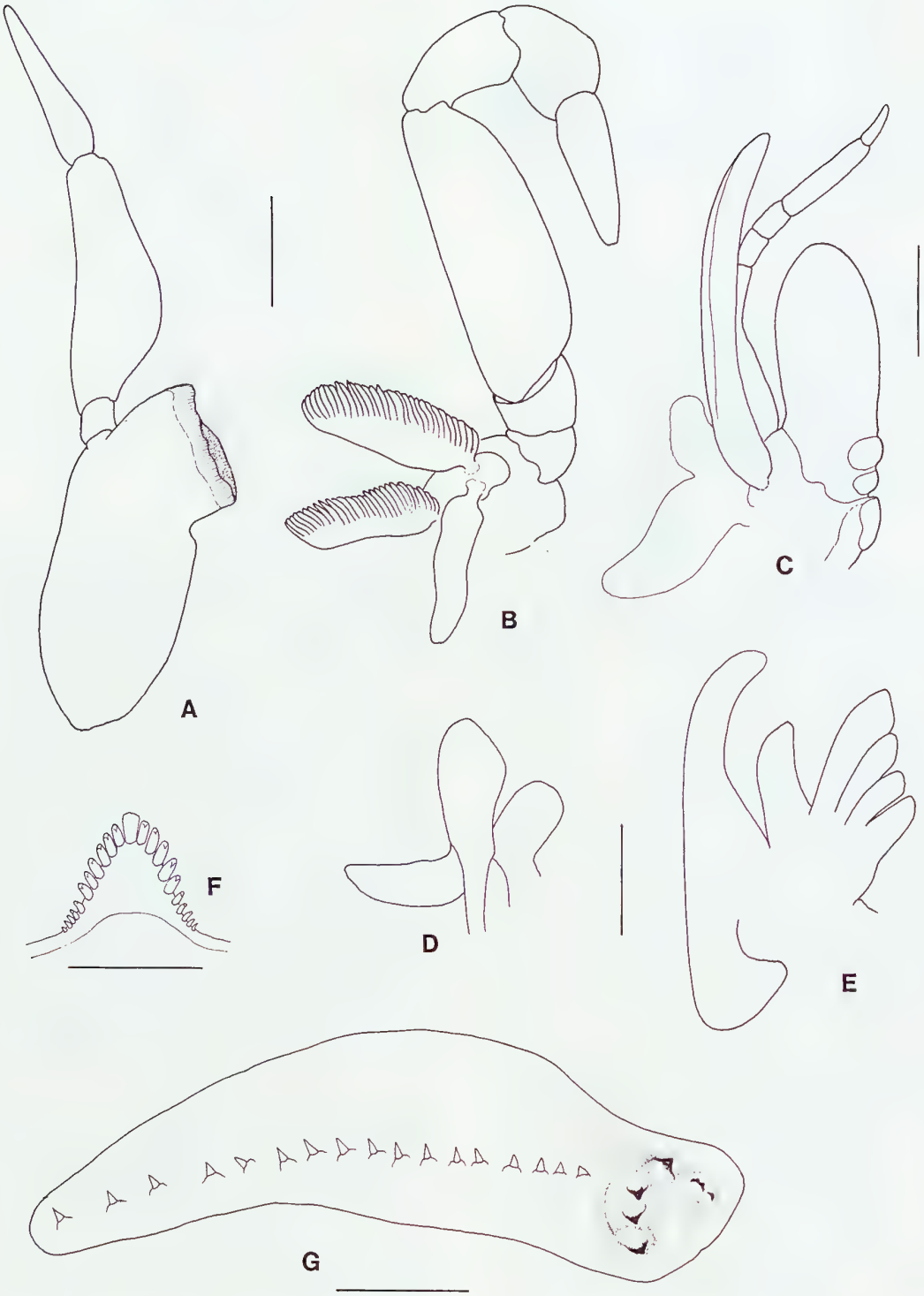

Fig. 2. *Haliporoides cristatus* n. sp. **A,** mandible; **B,** maxilliped 2; **C,** maxilliped 1; **D,** maxilla 1; **E,** maxilla 2; **F,** prepyloric ossicle; **G,** zygocardiac ossicle and cardiac plate. (Scales: A-E = 3 mm, F,G = 1 mm).

ending anterior to lateral spines; latter continuous with ridges flanking sulcus. Meisal uropodal ramus over-reaching telson by 0.4 of its own length; lateral ramus over-reaching inner by almost 0.3X its own length, bearing strong distolateral spine at about distal four-fifths. Pleopod 3–5 in male with rounded mediodorsal ridge; latter less marked in female.

Thelycum with sternite XII having sharp strongly raised median crest; sternite XIII with strong acute anteroventrally directed median spine and ridge; sternite XIV smoothly convex, bearing numerous short setules.

Petasma with ventromedian lobule distally narrowed, laterally curved, apically rounded. Dorsolateral lobule, margin distally oblique; ventrolateral lobule with distally free part falling considerably short of, and about twice width of distal free part of ventromedian lobule; distal margin curved mesially towards apex, ventral costa proximally broad, tapering distally along outer margin of lobule.

Appendix masculina about 1.5X longer than broad, distally narrowed, ventrally hollowed, lacking any setae. Appendix interna roughly subelliptical, falling short of, and tucked into ventral hollow of appendix masculina; dorsolateral spur short, bluntly triangular.

Remarks. (See Remarks section of following species).

Etymology. The specific name, from the Latin, meaning a crest, refers to the crested condition of the rostrum of this species.

Haliporoides sibogae australiensis n. ssp.

Figs 3, 4, 5A–F

Haliporus sibogae de Man, 1907: 138.
Haliporoides sibogae.—Grey, Dall & Baker, 1983: 15, 40, pls 3, 47.

Type material. New South Wales: HOLOTYPE: AM P34381, east of Broken Bay, 33°43–39′S 151°54–55′E, 477 m, demersal prawn trawl, *Kapala* (K83-14-07), 27 Oct 1983; 1 ♂, 31.5 mm. PARATYPES: AM P35891, east of Broken Bay, 33°43–39′S 151°54–55′E, 477 m, demersal prawn trawl, *Kapala* (K83-14-07), 27 Oct 1983; 1 ♂, 15.8 mm, 8 ♀, 15.6–39.5 mm. AM P33023, north-east of Port Jackson, 33°46–44′S 151°49–51′E, 425 m, demersal prawn trawl, *Kapala* (K80-21-04), 16 Dec 1980; 1 ♀. AM P30798, 32 km east of Greenwell Point, near Nowra, 34°55′S 151°08′E, 400 m, trawl, 16 July 1980; 1 ♀. AM P19149, south-east of Broken Bay, 33°42′S 151°55′E to 33°40′S 151°57′E, 810 m, demersal prawn trawl, *Kapala* (K72-07-16), 7 Dec 1972; 1 ♀, 39.3 mm. AM P21050, north-east of Wollongong, 34°16′S 151°26′E to 34°22′S 151°23′E, 356 m, demersal prawn trawl, *Kapala* (K75-05-01), 8 Aug 1975; 1 ♀, 31.0 mm. USNM 211389, north-east of Point Danger, 27°55–57′S 154°03′E, 629 m, *Kapala* (K78-23-09), 6 Nov 1978; 2 ♂, 26.3–26.5 mm. USNM 211388, east of Broken Bay, 33°43–39′S 151°54–55′E, 477 m, demersal prawn trawl, *Kapala* (83-14-07), 27 Oct 1983; 1 ♂, 15.4 mm, 5 ♀, 20.5–39.5 mm.

Additional material examined. New South Wales: AM G6049, 35 mi east of Sydney, 1434 m; 9 ♀. AM P4696, east of Sydney, 272 m, *Gunundaal,* May 1920; 1 ♀. AM P4697, east of Sydney, 272 m, *Gunundaal,* May 1920; 1 ♀. AM P18020, south-east of Sydney, 34°19–13′S 151°24–28′E, 351–360 m, bottom trawl, *Kapala* (K71-10-03), 28 June 1971; 1 ♀. AM P18025, east of Long Reef, 33°41–44′S 151°55–53′E, 570 m, bottom trawl, *Kapala* (K71-07-01), 20 Apr 1971; 19 ♀. AM P19150, south-east to east of Broken Bay, 33°43′S 151°55′E to 33°37′S 152°02′E, 675 m, demersal prawn trawl, *Kapala* (K72-06-04), 19 Oct 1972; 1 ♀. AM P19151, east of Wollongong, 34°16′S 151°26′E, 366 m, *Kapala* (K71-10-03), 28 June 1971; 1 ♀. AM P19152, east to north-east of Port Jackson, 33°51′S 151°51′E to 33°45′S 151°55′E, 675 m, demersal prawn trawl, *Kapala* (K72-06-03), 19 Oct 1972; 5 ♂. AM P19644, transect from east of Newcastle to east of Sydney, 33°00–44′S 151°50′–152°31′E, 365 m, July 1972; 5 ♂. AM P20804, south-east of Cape Howe, 37°45′S 150°12′E to 37°38′S 150°16′E, 416 m, demersal fish trawl, *Kapala* (K75-03-02), 11 July 1975; 2 ♂, 2 ♀. AM P21688, north-east of Yamba, 29°26′S 153°49′E to 29°20′S 153°50′E, 450 m, demersal prawn trawl, *Kapala* (K75-09-08), 12 Oct 1975; 1 ♂, 1 ♀. AM P21698, south-east of Cape Hawke, 32°22′S 152°58′E to 32°17′S 153°01′E, 463 m, demersal prawn trawl, *Kapala* (K75-08-03), 2 Oct 1975; 1 ♂. AM P33016, off Sydney, 33°46′S 151°50′E to 33°42′S 151°53′E, 414 m, demersal prawn trawl, *Kapala* (K80-06-01), 24 May 1980; 4 ♂, 1 ♀. AM P33032, north-east of Point Danger, 27°55′S 154°03′E to 27°57′S 154°03′E, 629 m, demersal prawn trawl, *Kapala* (K78-23-09), 6 Nov 1978; 3 ♂, 4 ♀. AM P32410, south-east of Newcastle, 32°59′S 152°34′E to 33°02′S 152°31′E, 360 m, demersal prawn trawl, *Kapala* (K77-23-08), 7 Dec 1977; 3 ♀. AM P33017, north-east of Point Danger, 28°01′S 154°00′E to 27°58′S 154°00′E, 542 m, demersal prawn trawl, *Kapala* (K78-17-10), 17 Aug 1978; 5 ♂, 14 ♀. AM P32411 and AM P32412, north-east of Jervis Bay, 34°50′S 151°15′, 801 m, benthic dredge, *Kapala* (K78-27-04), 12 Dec 1978; 1 ♂, 3 ♀. AM P33021, north-east of Wollongong, 34°21′S 151°25′E to 34°19′S 151°27′E, 432 m, demersal prawn trawl, *Kapala* (K78-27-13), 13 Dec 1978; 5 ♂, 4 ♀. AM P33018, south-east of Broken Bay, 33°40′S 151°54′E to 33°33′S 151°58′E, 450 m, demersal prawn trawl, *Kapala* (K74-15-25/26), 5 Dec 1974; 2 ♂, 1 ♀. AM P33019, north-east of Broken Bay, 33°29′S 152°07′E to 33°32′S 152°04′E, 594 m, demersal fish trawl, *Kapala* (K76-16-08), 14 Oct 1976; 2 ♂, 2 ♀. AM P33020, off Shoalhaven Bight, 34°54–57′S 151°12–11′E, 540 m, demersal prawn trawl, *Kapala* (K78-27-06), 12 Dec 1978; 5 ♂, 3 ♀. Victoria: AM E6124, 40 mi south south-east of Genoa Peak, 363 m, *Endeavour;* 1 ♂, 1 ♀. AM E4828, off eastern slope of Gabo Island, 363 m, Nov 1913; 1 ♀. AM P9640, Gabo Island to Everard Grounds, 400 m, *Endeavour,* 28 Oct 1914; 1 ♂. AMP9641, Gabo Island to Everard Grounds, 400 m, *Endeavour,* 28 Oct 1914; 1♀. AM P18021, south-east of Gabo Island, 37°39′S 150°17′E to 37°45′S 150°13′E, 396–401 m, danish trawl, *Kapala* (K71-13-02), 30 July 1971; 2 ♂, 2 ♀. AM P18024, south-east of Gabo Island, 37°42′S 150°16′E to 37°39′S 150°17′E, 387 m, *Kapala* (K71-13-01), 30 July 1971; 9 ♂, 10 ♀.

Description. Integument firm, with overall fine pile of very short setules. Rostrum reaching to

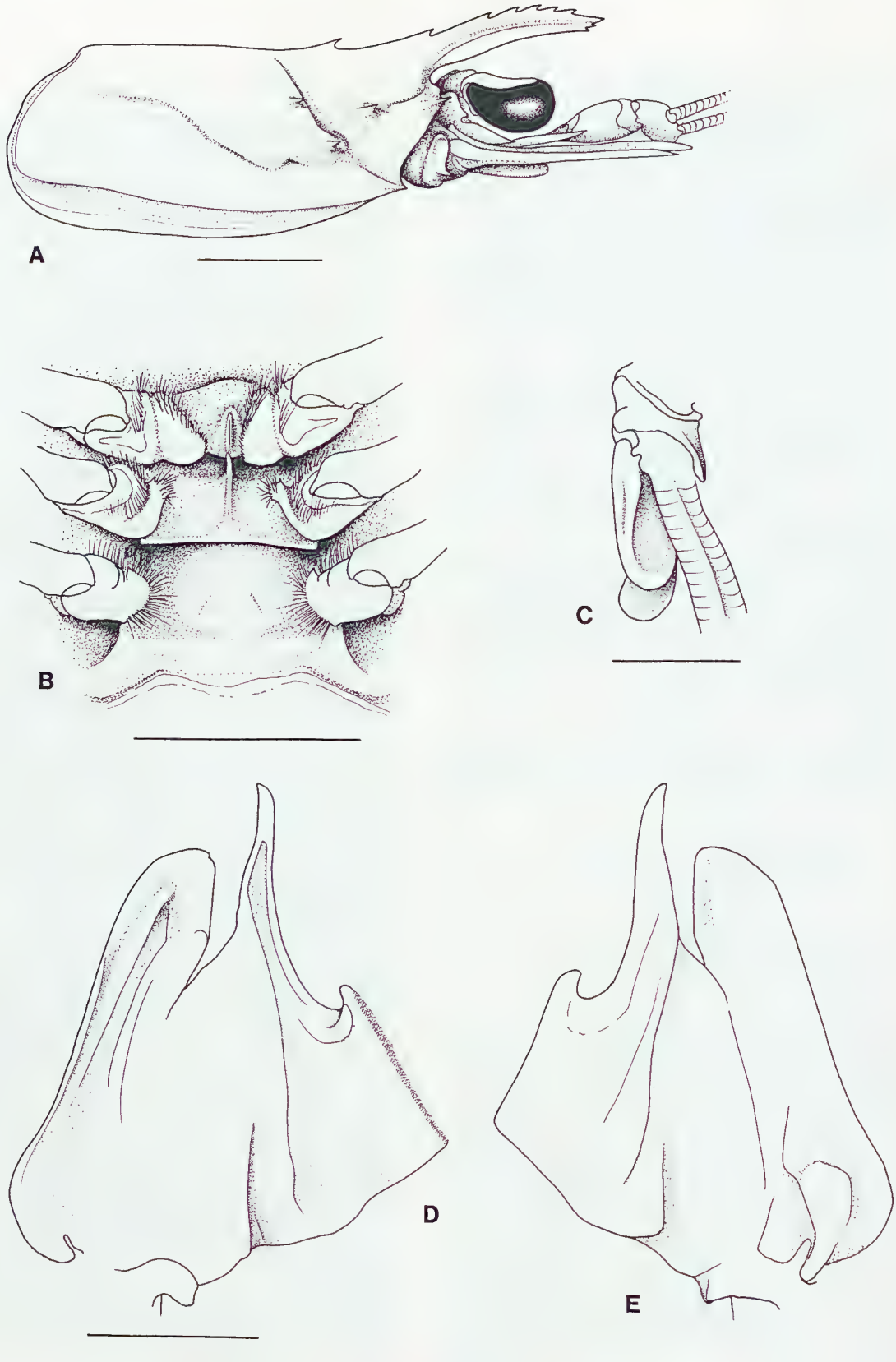

Fig. 3. *Haliporoides sibogae australiensis* n. ssp. **A,** carapace in lateral view; **B,** thelycum; **C,** pleopod 2 ♂, appendix masculina; **D,E,** petasma cl 28.3 mm. (Scales: A,B = 10 mm, C = 2 mm, D,E = 3 mm).

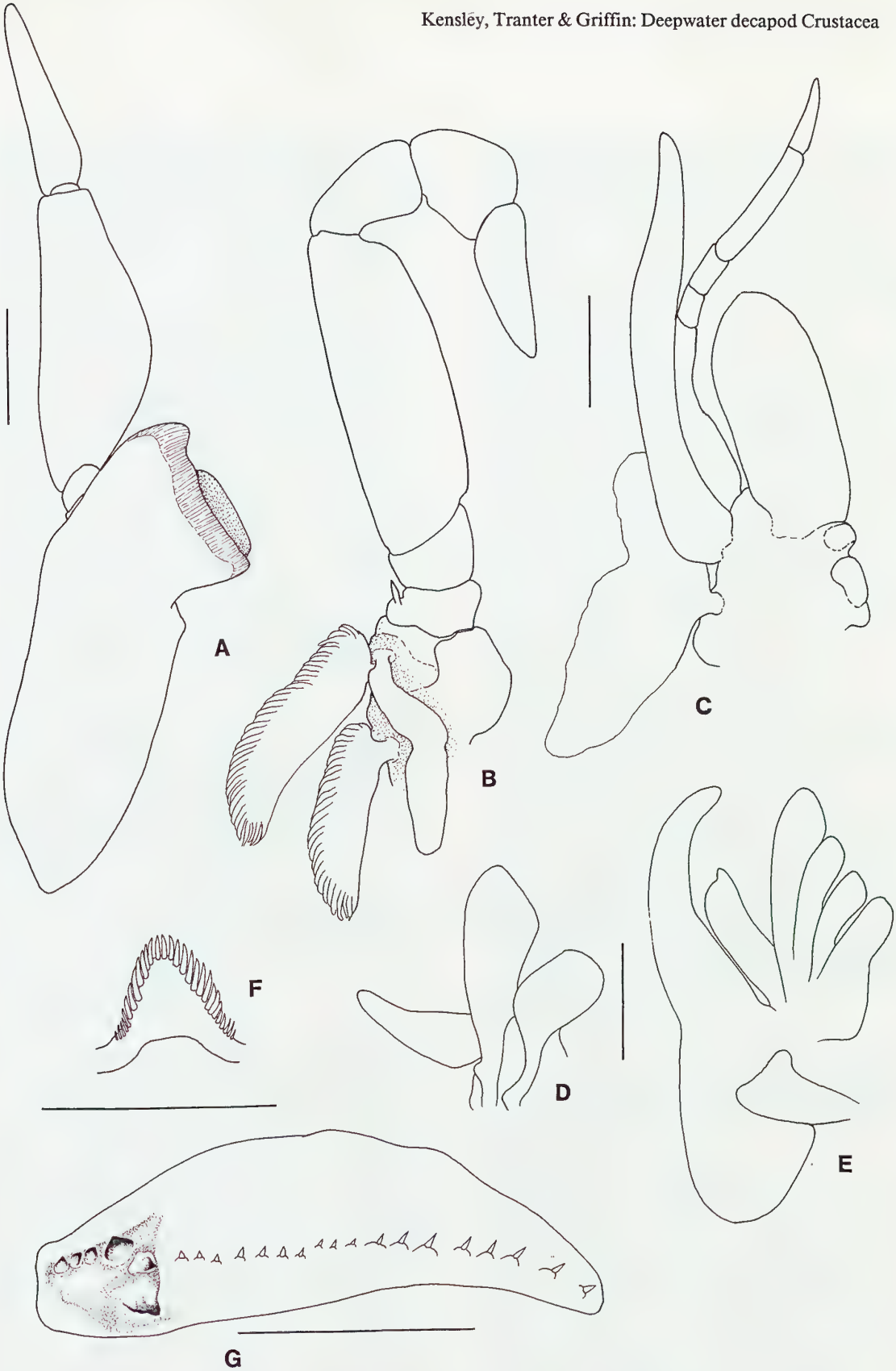

Fig. 4. *Haliporoides sibogae australiensis* n. ssp. **A,** mandible; **B,** maxilliped 2; **C,** maxilliped 1; **D,** maxilla 1; **E,** maxilla 2; **F,** prepyloric ossicle; **G,** zygocardiac ossicle and cardiac plate. (Scales: A-G = 3 mm).

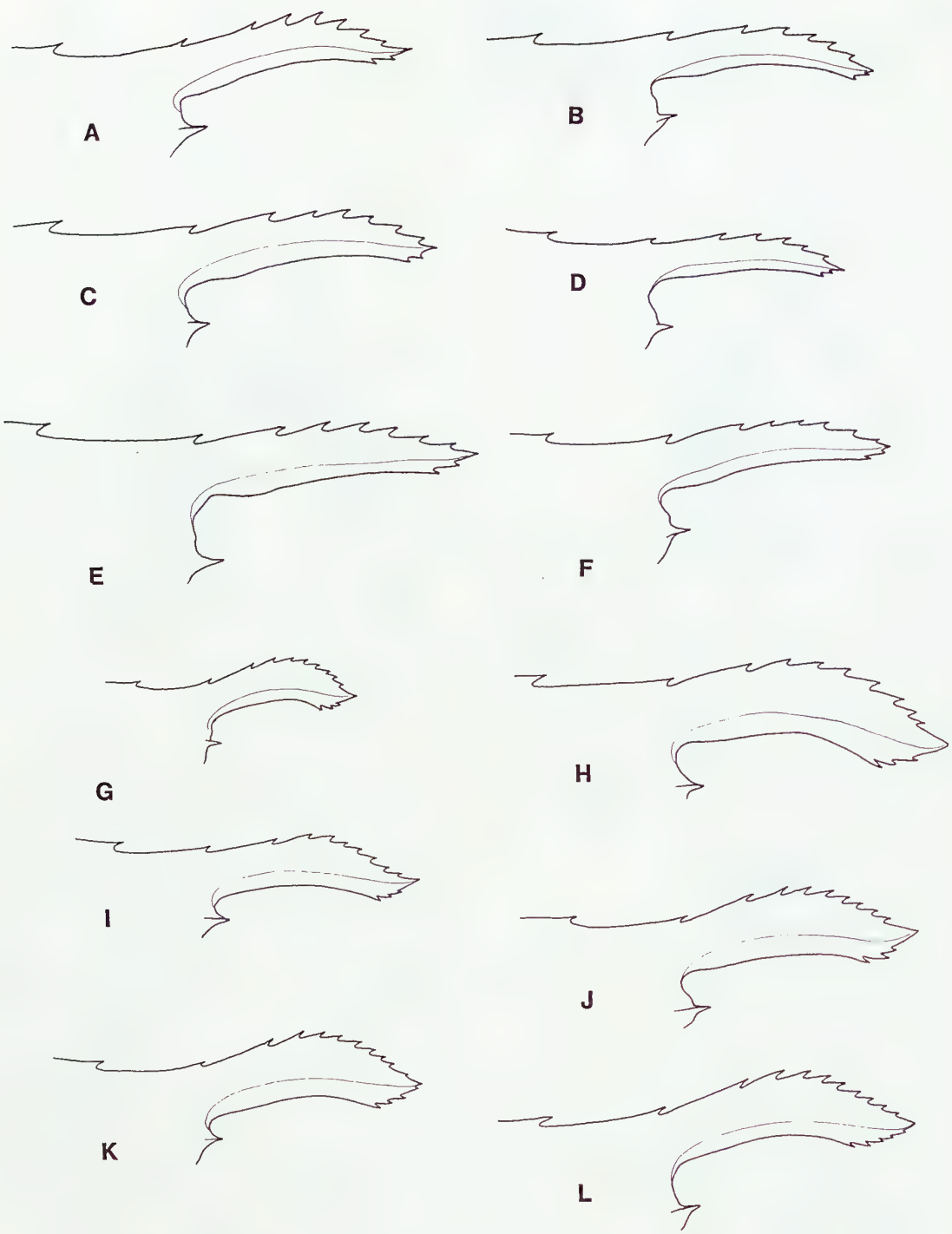

Fig. 5. Rostral variation. **A-F,** *Haliporoides sibogae australiensis* n. ssp. **A,** ♀ cl 29.9 mm; **B,** ♂ cl 27.6 mm; **C,** ♀ cl 33.9 mm; **D,** ♂ cl 28.1 mm; **E,** ♀ cl 35.0 mm; **F,** ♀ cl 29.0 mm; **G-L,** *Halioporoides cristatus* n. sp. **G,** ♂ cl 17.0 mm; **H,** ♀ cl 33.8 mm; **I,** ♂ cl 25.0 mm; **J,** ♀ cl 29.0 mm; **K,** ♀ cl 27.2 mm; **L,** ♀ cl 29.8 mm.

between midlength and distal margin of article 2 of antennular peduncle, subhorizontal to offset from carapace at angle of up to 30°, proximally low, tapering steadily to apex; straight to slightly arched over eye. Rostral and epigastic tooth-formula: $\frac{6+1}{1}$ to $\frac{8+1}{2}$; most frequent form $\frac{7+1}{2}$; epigastric tooth situated at about 2/7 length of carapace from orbital margin; first rostral tooth situated over orbital margin. Adrostral carina strong, acute, running from orbital margin to base of rostral apex. Postrostral carina barely marked, obsolete anterior to cervical groove. Pterygostomian spine strong, narrowly triangular, with distinct carina continuous with anteriorly acute hepatic carina. Hepatic sulcus fairly deep, becoming obsolete just ventral to mid-dorsal line. Suprahepatic spine equal in strength to hepatic spine. Posthepatic carina absent. Branchiocardiac carina rounded, sulcus relatively deep anteroventrally, becoming posterodorsally obsolete well before posterior carapace margin. Postorbital spine stronger than hepatic and suprahepatic spines, keeled. Submarginal carina acute, reaching and extending dorsally along posterior carapace margin. Low inconspicuous rounded mid-dorsal tubercle near posterior margin visible only in large adults (cl 30♀ mm).

Eyes as illustrated.

Antennular peduncle about 0.6X carapace length; prosartema falling short of distal margin of eye and well short of base of peduncle article 2; stylocerite short, basally broad, spine acute, not reaching midlength of basal antennular peduncle article. Inner antennular flagellum 6X carapace length; outer flagellum 7X carapace length.

Scaphocerite over-reaching antennular peduncle by about 1/5 of its own length; strongly rigid lateral margin ending in acute spine falling short of apex of blade. Antennal flagellum at least 8X carapace length.

Mouthparts as figured.

Mandibular palp, second article 2.5X longer than wide, widest proximally; distal article slender, tapering, about 3/5 length of proximal article. Maxilliped 3 reaching beyond antennular peduncle by length of dactylus; latter slightly more slender in female than in male; ischium with distoventral fixed spine. Pereopod 1 reaching by length of the finger beyond carpocerite; merus with distocentral movable spine and 3 fixed proximal spines; basis and ischium with ventrodistal fixed spine. Pereopod 2 reaching to base of antennular peduncle article 3 in male and female. Pereopod 3 reaching by length of fingers beyond antennular peduncle article 3 in male and female; coxal plate in female expanded mesially, anterior surface hollowed, posterior surface strongly convex. Pereopod 4 extending by length of dactylus and half of propodus beyond antennular peduncle in female, by length of dactylus and propodus in male. Pereopod 5 extending beyond antennular peduncle by length of dactylus, propodus and half of carpus in female, by dactylus, propodus, and distal ⅛ of carpus in male. Pereopods increasing in length posteriorly. Anteromesial spine on coxae of pereopods 3–5 in both sexes; in female, coxa 4 with largest spine; in male, spine on coxa 3 and 4 small, on 5 expanded anteroventrally, broad, flattened, distally rounded. Sternite XIII in male with midventrally directed strongly flattened spine.

Abdominal segments 4–6 mid-dorsally sharply keeled, ending posteriorly in very small spine. Abdominal segment 6 slightly longer than anterior width, ventral margin evenly convex, with single small denticle (sometimes absent) posteriorly. Telson with median sulcus deepest in anterior half, flattening out, ending at level of lateral spines; latter continuous with ridges flanking sulcus, posteriorly acute, anteriorly rounded. Mesial uropodal ramus over-reaching telson by ⅓ of its own length; lateral ramus over-reaching inner by about ¼ of its own length, bearing strong distolateral spine at about distal five-sixths. Pleopods 3–5 in male with narrowly rounded mediodorsal ridge; ridge almost as strong in female.

Thelycum with sternite XII bearing strong raised median crest; sternite XIII with strong acute anteroventrally directed median spine and ridge; sternite XIV evenly convex, sometimes with faint hint of median papilla.

Petasma with ventromedial lobule distally narrowed, almost straight, apically narrowly rounded; dorsolateral lobule margin distally oblique. Ventrolateral lobule with distally free, broad, apically rounded part falling considerably short of ventromedian lobule, about 2–2.5X width of ventromedian lobule at base; distal margin curved mesially towards apex, ventral costa proximally submarginal, distally becoming more acute and extending almost to middle of surface of free part of lobule.

Appendix masculina about twice longer than broad, distally narrowed, ventrally strongly hollowed, lacking setae. Appendix interna roughly rectangular, not reaching apex of, and tucked into ventral hollow of appendix masculina; dorsolateral spur short, bluntly triangular.

Remarks. The two species described above belong to the genus *Haliporoides* (sensu Pérez Farfante, 1977a) for possessing the following characters: epigastric tooth separated from rostral teeth by long interval; suprahepatic spine present; orbital spine lacking; ventral antennular flagellum subcylindrical; dorsal antennular flagellum subcylindrical; lateral ramus of uropod armed with distolateral spine; telson with single pair of fixed lateral spines; podobranchs restricted to maxilliped 2.

Pérez Farfante (1977a: 290) asserts that in the

Indo-West Pacific, *Haliporoides triarthrus* Stebbing, and *H. sibogae* (de Man) belong to this genus. Crosnier (1978), dealing with the *Hymenopenaeus* complex in Madagascar, recognised the following taxa: *Hymenopenaeus sibogae madagascariensis* Crosnier, *H. lucasi* Bate, *H. halli* Bruce, *H. propinquus* (de Man), *H. furici* Crosnier, and *H. triarthrus vinroi* Crosnier. Of these, *H. lucasi, H. halli, H. furici* and *H. propinquus* are true *Hymenopenaeus;* by Pérez Farfante's definition (1977a), the remainder are true *Haliporoides.*

Crosnier (1978) provides a table for comparing the *sibogae* complex of species and subspecies, to which group the two present species obviously belong. *Haliporoides sibogae madagascariensis* is distinguished from the typical form (recorded from Indonesia, Australia, Japan, New Zealand, and the Chinese Sea), by having a slightly (but still overlapping) higher rostral count, a postrostral carina extending beyond the cervical groove, and a slightly more elevated and proportionally deeper rostrum. It would seem that while *H. sibogae australiense* is closely related to the two *sibogae* forms, having a rostral formula very similar to the two previously recognised *H. sibogae* forms, a postrostral carina ending anterior to the cervical groove, a suprahepatic spine of equal strength to that of the hepatic spine, a female sternite XIV lacking a longitudinal ridge, a ventromedian lobule of the petasma slender but not distally bent, and slightly different appendix masculina and zygocardiac ossicle structure, it is sufficiently and constantly different to warrant subspecific separation.

Schmitt (1926), in recording *Haliporus sibogae* from Victoria, Australia, mentions the rostral formula as ranging from $\frac{7}{1}$ to $\frac{9}{2}$. Six specimens from the *Endeavour* material in the USNM collections were examined, as well as the *Endeavour* material in the Australian Museum. All belong to the present subspecies (see Material examined). The high-crested rostral form (*H. cristatus*) bears some superficial resemblance to *H. triarthrus triarthrus* and *H. triarthrus vinroi*, from the east coast of South Africa, Mozambique, and Madagascar, but differs in some major respects (see Table 1). These include the rostral formula (the African species never having more than three ventral teeth), the postrostral carina (which extends posteriorly to the cervical groove in *H. triarthrus*), the ventromedian lobule of the petasma (much broader in the African species) and the female sternite XIV (which has a distinct median raised area in *H. triarthrus*). On the basis of these characters, *H. cristatus* can easily be separated from *H. triarthrus.*

Potter & Dredge (1985: 226) refer to an undescribed species of *Haliporoides* taken in southern and central Queensland waters, and also recorded from off New South Wales. This species, which is *H. cristatus,* "... is separated from *H. sibogae* by its yellowish hue, the greater curvature of the rostrum, and the distinctive white stripe on the dorsal portion of the uropod."

Hymenopenaeus Smith, 1882

Hymenopenaeus halli Bruce

Hymenopenaeus halli Bruce, 1966: 216, figs 1, 2.—Crosnier, 1978: 120, figs 39d, 40d, 42c, 43b, 45a–d, 46b, c.

Material examined. New South Wales: AM P33198, off New South Wales coast, demersal prawn trawl, *Kapala* (K78-23), Nov 1978; 1 ♂, 3 ♀. AM P33199, 33°47′S 151°55′E to 33°44′S 151°57′E, 890–900 m, demersal prawn trawl, *Kapala* (K78-28-16), 7 Dec 1978; 1 ♂, 2 juvs.

Diagnosis. Rostrum slender, straight, directed slightly obliquely, with 5–7 dorsal teeth well separated from 2 postrostral teeth; antennal,

	H. sibogae	*H. sibogae madagascariensis*	*H. triarthrus vinroi*	*H. sibogae australiensis*	*H. cristata*
Rostral formula (most frequent form in parentheses)	5+2/1 to 7+2/2 (5+2/2)	6+2/2 to 8+2/2 (6+2/2, 7+2/2)	8+2/2 to 12+2/2 (9+2/2)	5+2/1 to 6+2/2 (6+2/1)	7+2/3 to 9+2/3 (9+2/3)
Rostral shape	low, gentle curved	low, almost straight	high crested	low, almost straight to gently curved	high crested
Postrostral carina	stopping just anterior to cervical groove	ending posterior to cervical groove, half way to posterior margin	ending posterior to cervical groove, midway to posterior margin	ending anterior to cervical groove	ending anterior to cervical groove
Suprahepatic spine + Stermote XIV	small with longitudinal swelling	small with strong longitudinal swelling	minuscule almost indiscernible longitudinal swelling	= hepatic spine no longitudinal swelling	= hepatic spine no longitudinal swelling
Ventromedial lobule of petasma	short, pointed, ear-shaped	elongate (variable) pointed	broad, rounded	relatively elongate, rounded to subacute	relatively elongate, rounded
Lateral process of petasma	broad	broad	broad	moderately broad	narrow

Table 1. Comparison of five Indo-Pacific species of *Haliporoides.*

postantennal, hepatic, and branchiostegal spines present. Prosartema well developed; antennular flagella filiform, cylindrical. Telson with single pair of fixed lateral spines. Petasma with ventromedian lobule distally divided by deep slit into 2 subequal apically acute processes. Thelycum with sternal plate between bases of pereopod 5 having prominent medio-longitudinal ridge.

Distribution. Off Madagascar, Indonesia, South China Sea; 540–910 m.

Hymenopenaus lucasi (Bate)

Solenocera lucasii Bate, 1881: 185.
Hymenopenaeus lucasi.—Crosnier, 1978: 115, figs 37f–h, 39c, 40c, 42d, 43a, 44, 46a.

Material examined. New South Wales: AM P33163, north-east of Danger Point, 27°55′S 154°03′E to 27°57′S 154°03′E, 629 m, demersal prawn trawl, *Kapala* (K78-23-09), 6 Nov 1978; 1 ♀.

Diagnosis. Rostrum short, horizontal, with 6 or 7 dorsal teeth, of which 3 or 4 posterior to orbital margin but not separated by marked gap; ventrally convex but unarmed. Petasma with mesial process distally tapering, apically rounded; lateral process much shorter than mesial, distally truncate; lateral flap broadly convex. Thelycum with sternite between bases of pereopod 3 bipartite, with rounded anterior part and posterior ovate and medially ridged portion; sternite between pereopod 4 anterior rounded, posteriorly bilobed; sternite of pereopod 5 ovate.

Distribution. Madagascar, Seychelles, Maldives, Indonesia, Japan; 200–629 m.

Hymenopenaeus propinquus (de Man)

Haliporus propinquus de Man, 1907: 140.
Hymenopenaeus propinquus.—Crosnier, 1978: 124, figs 39e, 40e, 42e, 43c, 45e–h, 46d, e, 47a.

Material examined. New South Wales: AM P25130, east of Broken Bay, 33°35′S 152°01′E to 33°32′S 152°03′E, 810 m, demersal prawn trawl, *Kapala* (K76-24-03), 20 Dec 1976; 1 ♀. AM P25140, east of Broken Bay, 33°35′S 152°01′E to 33°32S 152°03′E, 810 m, demersal prawn trawl, *Kapala* (K76-24-03), 20 Dec 1976; 6 ♂, 3 ♀. AM P26761, north-east of Norah Head, 33°11′S 152°24′E to 33°09′S 152°25′E, 720 m, demersal prawn trawl, *Kapala* (K77-23-10), 7 Dec 1977; 1 ♂, 3 ♀. AM P26774, south-east of Broken Bay, 33°40′S 151°56′E to 33°37′S 151°56′E, 711 m, demersal prawn trawl, *Kapala* (K77-23-06), 6 Dec 1977; 1 ♂, 6 ♀, 2 juvs. AM P26802, north-east of Norah Head, 33°08′S 152°27′E to 33°10′S 152°24′E, 580 m, demersal prawn trawl, *Kapala* (K77-23-09), 7 Dec 1977; 1 ♀. AM P26814, north-east of Norah Head, 33°08′S 152°27′E to 33°10′S 152°24′E, 580 m, demersal prawn trawl, *Kapala* (K77-23-09), 7 Dec 1977; 4 ♂, 12 ♀. AM P33014, north-east of Broken Bay, 33°27′S 152°09′E to 33°25′S 152°11′E, 874 m, demersal prawn trawl, *Kapala* (K77-23-13), 8 Dec 1977; 1 ♂, 2 ♀. AM P33013, east of Broken Bay, 33°35′S 152°00′E to 33°33′S 152°02′E, 810 m, demersal prawn trawl, *Kapala* (K77-23-12), 8 Dec 1977; 1 ♂, 1 ♀. AM P33012, north-east of Point Danger, 28°03′S 154°04′E to 28°01′S 154°04′E, 724 m, demersal prawn trawl, *Kapala* (K78-23-08), 6 Nov 1978; 9 ♂, 1 ♀. AM P33015, east of Broken Bay, 33°32′S 152°06′E to 33°334′S 152°05′E, 810 m, demersal prawn trawl, *Kapala* (K79-20-13), 6 Dec 1979; 1 ♀. AM P35918, south-east of Broken Bay, 33°43′S 151°56′E to 33°39′S 151°58′E, 631 m, demersal fish trawl, *Kapala* (K84-16-03), 25 Sept 1984; 3 ♂, 2 ♀.

Diagnosis. Rostrum slender, directed obliquely upward, armed dorsally with 6 teeth separated by marked gap from 2 postrostral teeth. Petasma with mesial process extending well beyond lateral process, distally rounded, lacking marginal spines at apex; lateral process broadly triangular. Thelycum with sternite between pereopod 4 with transverse rounded setose swelling anteriorly and rounded lateral process posteriorly; sternite between pereopods 5 more or less hemispherical, with anterior margin faintly sinuous, posteriorly broadly rounded, surface with 2 submedian depressions.

Distribution. Gulf of Aden, Zanzibar, Reunion, Madagascar, Maldives, Indonesia; 510–1080 m.

Solenocera Lucas, 1849

Solenocera choprai Nataraj

Solenocera choprai Nataraj, 1945: 91, figs 1–4.—Crosnier, 1978: 141, figs 49g, 51d, e, 52c, 53a–c, 54a, b, 55c, 56a–e, 58c, 59f; Grey, Dall & Baker, 1983: 42, pl. 4 (pl. 4 in this reference is of *Solenocera alticarinata* Kubo, 1949).

Material examined. New South Wales: AM P32479, east of Danger Point, 28°16′S 153°50′E to 28°12′S 153°51′E, 144 m, trawl, *Kapala* (K78-09-08), 2 June 1978; 1 ♂, 1 ♀, 1 juv.

Diagnosis. Rostrum not reaching beyond eye, ventrally gently convex, dorsally with 8 teeth, 4 of which postorbital. Carapace lacking pterygostomian spine; inferior margin of hepatic groove anterior to hepatic spine ending in small excavate area; mid-dorsal carina posterior to cervical groove lamelliform. Petasma with distal process of ventromedian lobule not markedly extending beyond dorsolateral lobule; both fringed distally with spines. Thelycum in female consisting of rectangular hollow between bases of pereopod 5.

Distribution. Gulf of Suez, Arabian Sea, Madagascar, India, north-western Australia, China Sea; 50–175 m.

Solenocera faxoni de Man

Solenocera faxoni de Man, 1907: 136; 1911: 52, pl. 5, fig. 13.—Kubo, 1949: 241, figs 8U, 20P, 27C–E, 45F, 66A, B, 72R,X, 80C, 97, 98E–G, 100.

Material examined. New South Wales: AM P32475, east of Terrigal, 33°26′S 152°05′E, 396 m, prawn trawl,

Kapala (K79-08-08), 18 July 1979; 1 ♀. AM P32476, east of Charlotte Head, 32°17′S 153°01′E, 360 m, prawn trawl, *Kapala* (K78-03-03), 5 Apr 1978; 1 ♂. AM P32477, east of North Solitary Is., 29°56′S 153°41′E to 29°53′S 153°41′E, 360 m, demersal prawn trawl, *Kapala* (K78-06-01), 25 Apr 1978; 2 ♂. AM P32480, east of Point Danger, 28°05′S 153°58′E, 405 m, trawl, *Kapala* (K78-09-04), 1 June 1978; 5 ♂, 6 ♀.

Diagnosis. Rostrum barely reaching as far as eye, ventrally convex, unarmed, dorsally with 6 teeth of which 3–4 postorbital. Carapace tomentose only in region of rostrum; with hepatic, postorbital, and antennal spines present, pterygostomina spine absent; inferior margin of hepatic groove anterior to hepatic spine markedly raised, ending anteriorly in broadly flattened acute branchiostegal spine overlapping sterygostomian margin. Thelycum between bases of pereopods 4 and 5 simple deep hollow, demarked anteriorly by lateral ridge, meeting anteromesially as narrow laterally acute contiguous lobes between bases of pereopod 4.

Distribution. Indonesia, Japan; 250–310 m.

Solenocera rathbuni Ramadan

Solenocera rathbuni Ramadan, 1938: 57.—Crosnier, 1978: 163, figs 49e, 52f, 55f, 57c, 59b,i, 62a–c, 63a–d.

Material examined. New South Wales: AM P32482, east of Point Danger, 28°16′S 153°50′E, 137 m, trawl, *Kapala* (K78-09-09), 2 June 1978; 1 ♀. AM P32483, east of Point Danger, 28°05′S 153°49′E, 137 m, trawl, *Kapala* (K78-09-14), 3 June 1978; 7 ♂, 13 ♀.

Diagnosis. Postrostral carina almost reaching posterior margin of carapace; pterygostomian and branchiostegal spines absent; anterior hepatic carina straight or very faintly sinuous, ending just short of carapace margin, not reflexed. Abdominal somite 1 rounded; somite 2 with faint mid-dorsal ridge; somites 3–6 strongly carinate, somite 6 with mid-dorsal spine on posterior margin. Petasma with distal process of ventromedian lobule extending well beyond dorsolateral lobule, both fringed with spinules; ventral costa distally rounded. Dorsolateral lobule distally fringed with spinules; ventrolateral lobule distally rounded. Thelycum with sternite XII having posterolateral raised tubercle bearing spine, hollowed area of coxa articulating on anterior face of tubercle. Sternite XIII similar to sternite XII. Sternite XIV with 2 low submedian setose patches near anterior margin; strong apically bifid tubercle at mid-sternite; posterior margin with median furrow and raised roughly rectangular lateral plate.

Remarks. The present material is all considerably larger than that reported by Crosnier (1978) from Madagascar (8.2–10.5 mm cl, as against 17.5–25.8 mm cl). The lectotype from Hawaii, too, has a carapace length of only 9.3 mm.

The rostrum, carapace, the pterygostomian region, and the antennular flagellar apices all agree with Crosnier's description. Slight differences in the thelycum can be detected. Crosnier figures sternite XIV as having two well separated submedian tubercles and a lower anteromedian tubercle. In the present material, these three tubercles are situated closer together, on a large median boss.

Crosnier (1978) provides several dimensions characteristic of *S. rathbuni*. In all four of his specimens, the ratio of length of superior antennular flagellum to carapace length is always 1.3 or more. In the present material, this ratio ranges from 0.78–0.94 in females, 0.92–1.0 in males. This difference may be due to the immaturity of the Malagasy specimens. In Crosnier's material, the number of articles in the inferior antennular flagellum was 55–58 in males, 55–59 in females. In the present material, male counts range from 49–56, female counts 49–62.

Distribution. Madagascar, Hawaii; 80–110 m.

Family ARISTEIDAE

Subfamily BENTHESICYMINAE

Benthesicymus Bate, 1881

Benthesicymus investigatoris Alcock & Anderson

Benthesicymus investigatoris Alcock & Anderson, 1899: 282.—Crosnier, 1978: 21, figs 7c, d, 8c, d, 9, 10.

Material examined. New South Wales: AM P33024, south-east of Broken Bay, 33°39′S 152°06′E to 33°37′S 152°07′E, 990 m, demersal prawn trawl, *Kapala* (K79-20-15), 6 Dec 1979; 2 specimens.

Diagnosis. Podobranchs present on maxillipeds 2 and 3, and on pereopods 1–3. Telson with 4 pairs of movable lateral spines. Rostrum short, apically acute, with 2 dorsal teeth. Abdominal segment 5 ending posteriorly in tiny mediodorsal tooth. Thelycum of female with raised triangular area on sternite 12; sternite 13 with subcircular shield having rounded posteromedial process and 2 anterolateral subacute processes. Petasma of male distally expanded, broadly oval, distal margin lacking lobes.

Distribution. Indo-West Pacific: Hawaii, Fiji, Japan, Indonesia, Philippines, Andaman Sea, Gulf of Manrar, Saya de Malha, east Africa from Somalia to South Africa, Madagascar; 600–1525 m.

Gennadas Bate, 1881

Gennadas bouvieri Kemp

Gennadas bouvieri Kemp, 1909: 726, pl. 74, figs 1–4, pl. 75, figs 6, 7.—Kensley, 1971: 273, fig. 1; Crosnier, 1978: 34, figs 15a, 18a, b; Griffiths & Brandt, 1983: 614.

Material examined. New Caledonia: AM P32898, east of New Caledonia, 21°05′S 166°45′E, 0–925 m,

midwater trawl, *Kimbla* (K4/71-5), 9 May 1971; 2 specimens. AM P32899, east of New Caledonia, 22°03′S 167°44′E, 0–800 m, midwater trawl, *Kimbla* (K4/71-11), 13 May 1971; 4 specimens.

New South Wales: AM P26590, south-east of Wollongong, 34°40′S 151°15′E to 34°35′S 151°17′E, 540 m, midwater trawl, *Kapala* (K77-19-05), 3 Nov 1977; 1 specimen. AM P32894, north-east of Broken Bay, 33°31′S 152°20′E to 33°28′S 152°22′E, 569 m, midwater trawl, *Kapala* (K77-24-02), 12 Dec 1977; 2 specimens. AM P32893, north-east of Broken Bay, 33°27′S 152°30′E to 33°23′S 152°32′E, 630 m, midwater trawl, *Kapala* (K77-24-03), 13 Dec 1977; 3 specimens. AM P32895, south-east of Norah Head, 33°20′S 152°32′E to 33°24′S 152°31′E, 360 m, midwater trawl, *Kapala* (K77-24-09), 14 Dec 1977; 3 specimens. AM P32892, north-east to east of Broken Bay, 33°28′S 152°34′E to 33°36′S 152°35′E, 630 m, midwater trawl, *Kapala* (K77-24-10), 14 Dec 1977; 8 specimens. AM P32896, north-east to east of Wollongong, 34°20′S 151°56′E to 34°25′S 151°54′E, 630 m, midwater trawl, *Kapala* (K77-24-12), 14 Dec 1977; 2 specimens. AM P32897, north-east of Norah Head, 33°05′S 153°05′E to 33°13′S 153°05′E, 630 m, midwater trawl, *Kapala* (K79-19-03), 28 Nov 1979; 1 specimen.

Diagnosis. Antennal angle acute, infra-antennal angle quadrate. Thelycum of female with sternite 13 with rounded flap lifting posteriorly, flanked by small lateral process; sternite 14 with broad oval shield having elongate process on anterolateral corners. Petasma of male with external lobe bipartite, both lobules acute; median lobe bipartite, both lobes acute, directed towards each other; internal lobe low; accessory lobe broadly oval.

Remarks. Griffiths & Brandt (1983) record this species associated with a warm-core eddy off eastern Australia.

Distribution. Caribbean; west coast of South Africa; Indo-Pacific; 250–630 m.

Gennadas capensis Calman

Gennadas capensis Calman, 1925: 5, pl. 1, figs 1, 2.– Kensley, 1971: 277, fig. 3; Crosnier, 1978: 36, fig. 18c.

Material examined. New Caledonia: AM P32886, east of New Caledonia, 22°03′S 167°44′E, 0–800 m, midwater trawl, *Kimbla* (K4/71-11), 13 May 1971; 8 specimens.

New South Wales: AM P32885, south-east of Port Jackson, 34°05′S 151°55′E to 34°10′S 152°14′E, 0–950 m, midwater trawl, *Kapala* (JP71-6), 25 Mar 1971; 5 specimens. AM P26600, north-east of Cape Howe, 37°24′S 150°30′E to 37°28′S 150°33′E, 540 m, midwater trawl, *Kapala* (K77-19-03), 1 Nov 1977; 6 specimens. AM P26588, south-east of Wollongong, 34°40′S 151°15′E to 34°35′S 151°17′E, 540 m, midwater trawl, *Kapala* (K77-19-05), 3 Nov 1977; 2 specimens. AM P32881, north-east of Broken Bay, 33°31′S 152°20′E to 33°28′S 152°22′E, 569 m, midwater trawl, *Kapala* (K77-24-02), 12 Dec 1977; 4 specimens. AM P32880, east of Broken Bay, 33°27′S 152°30′E to 33°23′S 152°32′E, 630 m, midwater trawl, *Kapala* (K77-24-03), 13 Dec 1977; 13 specimens. AM P32882, north-east to east of Broken Bay, 33°28′S 152°34′E to 33°36′S 152°35′E, 630 m, midwater trawl, *Kapala* (K77-24-10), 14 Dec 1977; 13 specimens. AM P32884, north-east of Norah Head, 33°05′S 153°05′E to 33°13′S 153°05′E, 630 m, midwater trawl, *Kapala* (K79-19-03), 28 Nov 1979; 3 specimens.

Diagnosis. Antennal angle acute, infra-antennal angle quadrate. Thelycum of female with W-shaped process on sternite 13, with median apex formed by concave process. Coxa of pereopod 2 bearing posteriorly-directed spoon-shaped process. Petasma of male with external lobe acute, triangular, with smaller scute lobule on median margin; median lobe truncate; internal lobe of 2 bluntly rounded lobules; accessory lobe low, bipartite.

Distribution. Caribbean; north-eastern Atlantic; west coast of South Africa; Indian Ocean; 250–630 m.

Gennadas gilchristi Calman

Gennadas gilchristi Calman, 1925: 6, pl. 1, figs 3, 4.— Kensley, 1971: 272, 273, 280, fig. 6; Griffiths & Brandt, 1983: 612, 614.

Material examined. New Caledonia: AM P32879, east of New Caledonia, 21°05′S 166°45′E, 0–925 m, midwater trawl, *Kimbla* (K4/71-5), 9 May 1971; 1 specimen.

New South Wales: AM P32877, south-east of Port Jackson, 34°05′S 151°55′E to 34°10′S 51°14′E, 0–950 m, midwater trawl, *Kapala* (JP71-6), 25 Mar 1971; 221 specimens. AM P32878, south-east of Port Jackson to north-east of Wollongong, 34°02′S 152°12′E to 34°14′S 152°14′E, 0–600 m, midwater trawl, *Kapala* (JP71-8), 25–26 Mar 1971; 3 specimens. AM P32866, south-east of Norah Head, 33°20′S 152°32′E to 33°24′S 152°31′E, 360 m, midwater trawl, *Kapala* (K77-24-09), 14 Dec 1977; 153 specimens. AM P32869, north-east of Broken Bay, 33°27′S 152°30′E to 33°23′S 152°32′E, 630 m, midwater trawl, *Kapala* (K77-24-03), 13 Dec 1977; 30 specimens. AM P32870, north-east to east of Broken Bay, 33°28′S 152°34′E to 33°36′S 152°35′E, 630 m, midwater trawl, *Kapala* (K77-24-10), 14 Dec 1977; 98 specimens. AM P32868, north-east of Broken Bay, 33°31′S 152°20′E to 33°28′S 152°22′E, 569 m, midwater trawl, *Kapala* (K77-24-02), 12 Dec 1977; 30 specimens. AM P32867, north-east to east of Wollongong, 34°20′S 151°56′E to 34°25′S 252°54′E, 630 m, midwater trawl, *Kapala* (K77-24-12), 14 Dec 1977; 19 specimens. AM P26589, P26591, south-east of Wollongong, 34°40′S 151°15′E to 34°35′S 151°17′E, 540 m, midwater trawl, *Kapala* (K77-19-05), 3 Nov 1977; 10 specimens. AM P26592, P26593, P32873, north-east of Batemans Bay, 35°36′S 150°55′E to 35°39′S 150°56′E, 540 m, midwater trawl, *Kapala* (K77-18-05), 27 Oct 1977; 11 specimens. AM P26595, north-east of Wollongong, 34°10′S 152°04′E to 34°12′S 152°02′E, 540 m, midwater trawl, *Kapala* (K77-18-01), 26 Oct 1977; 6 specimens. AM P26601, north-east of Cape Howe, 37°24′S 150°30′E to 37°28′S 150°33′E, 540 m, midwater trawl, *Kapala* (K77-19-03), 1 Nov 1977; 21 specimens. AM P32865, north-east of Norah Head, 33°05′S 153°05′E to 33°13′S 153°05′E, 630 m, midwater

trawl, *Kapala* (K79-19-03), 28 Nov 1979; 37 specimens. AM P32872, south-east of Newcastle, 33°03′S 152°58′E to 32°59′S 153°03′E, 482 m, midwater trawl, *Kapala* (K79-19-02), 27 Nov 1979; 5 specimens. AM P32874, north-east of Norah Head, 33°08′S 152°48′E to 33°16′S 152°46′E, 630 m, midwater trawl, *Kapala* (K79-19-10), 29 Nov 1979; 1 specimen. AM P32876, east of Newcastle, 32°51′S 153°01′E to 32°59′S 152°54′E, 540 m, midwater trawl, *Kapala* (K79-19-08), 29 Nov 1979; 3 specimens. AM P32871, south-east of Norah Head, 33°23′S 152°37′E to 33°19′S 152°39′E, 666 m, midwater trawl, *Kapala* (K77-24-06), 13 Dec 1977; 1 specimen. AM P11487, 4.8 km east of Port Hacking, 200 m, haul 200/39, net 100, K. Sheard, CSIRO Fisheries Section, 6 July 1939; 1 specimen.

Diagnosis. Antennal and infra-antennal angles of carapace narrowly rounded. Thelycum of female with sternite 13 having bilobed process. Petasma of male with external lobe acute, median lobe of 2 diverging lobules, internal lobe acute, accessory lobe distally broadly rounded.

Remarks. This would appear to be the commonest species of *Gennadas* in Australian waters. Griffiths & Brandt (1983) give an account of its occurrence and abundance in a warm-core eddy in the Tasman Sea off eastern Australia, where it was more abundant outside and at the edge of the eddy than inside.

Of the material in the Australian Museum, 12 specimens were heavily parasitised by a nematode within the carapace. It is possible that this *Gennadas* is the intermediate host for some parasitic nematode of fish.

Distribution. Off the west coast of South Africa; Agulhas Basin; southern Indian Ocean; off eastern Australia; 100–1000 m.

Gennadas incertus (Balss)

Amalopenaeus incertus Balss, 1927: 265, figs 24–29.
Gennadas incertus.—Kensley, 1971: 284, fig. 7; Crosnier, 1978: 37, figs 15b, 19a; Griffiths & Brandt, 1983: 614.

Material examined. New Caledonia: AM P35742, east of New Caledonia, 21°05′S 166°45′E, 0–925 m, midwater trawl, *Kimbla* (K4/71-5), 9 May 1971; 5 specimens.

New South Wales: AM P35738, south-east of Port Jackson, 34°05′S 151°55′E to 34°10′S 152°14′E, 0–950 m, midwater trawl, *Kapala* (JP71-6), 25 Mar 1977; 1 specimen. AM P35739, east of Broken Bay, 33°33′S 152°18′E to 33°31′S 152°18′E, 216 m, midwater trawl, *Kapala* (K77-24-01), 12 Dec 1977; 1 specimen. AM P35740, south-east of Norah Head, 33°20′S 152°32′E to 33°24′S 152°31′E, 360 m, midwater trawl, *Kapala* (K77-24-09), 14 Dec 1977; 3 specimen. AM P35741, north-east to east of Wollongong, 34°20′S 151°56′E to 34°25′S 151°54′E, 630 m, midwater trawl, *Kapala* (K77-24-12), 14 Dec 1977; 1 specimen.

Diagnosis. Antennal and infra-antennal angles of carapace acute. Thelycum of female with large concave shield on sternite 12, shield on sternite 13 with acute anterolateral corners, sternite 14 with broad oval shield with anterior and posterior notch. Petasma of male with external lobe of 2 large diverging lobules, median lobe of slender outer and broad inner lobule, internal lobe simple, rounded, accessory lobe rounded, reaching as far as median and internal lobes.

Remarks. Griffiths & Brandt (1983) record this species associated with a warm-core eddy off eastern Australia.

Distribution. North east and north west Pacific; Indian Ocean; west coast of South Africa; 100–900 m.

Gennadas kempi Stebbing

Gennadas kempi Stebbing, 1914: 283, pl. 27.—Kensley, 1971: 285, fig. 8; Griffiths & Brandt, 1983: 614.

Material examined. New Caledonia: AM P32917, east of New Caledonia, 21°05′S 166°45′E, 0–925 m, midwater trawl, *Kimbla* (K4/71-5), 9 May 1971; 2 specimens.

New South Wales: AM P32916, north-east of Cape Howe, 37°24′S 150°30′E to 37°28′S 150°33°E, 540 m, midwater trawl, *Kapala* (K77-19-03), 1 Nov 1977; 1 specimen. AM P32914, north-east of Broken Bay, 33°31′S 152°20′E to 33°28′S 152°22′E, 569 m, midwater trawl, *Kapala* (K77-24-02), 12 Dec 1977; 2 specimens. AM P32915, north-east of Broken Bay, 33°27′S 152°30′E to 33°23′S 152°32′E, 630 m, midwater trawl, *Kapala* (K77-24-03), 13 Dec 1977; 1 specimen.

Diagnosis. Antennal and infra-antennal angles of carapace rounded. Thelycum of female with triangular shield on sternite 12, rectangular shield on sternite 13, pentagonal shield on sternite 14. Petasma of male with acute external lobe, broad truncate median lobe, rounded internal lobe, accessory lobe rounded, flap-like.

Remarks. Griffiths & Brandt (1983) record this species associated with a warm-core eddy of eastern Australia.

Distribution. South west coast off South Africa; Indian Ocean; east coast of Australia; 250–800 m.

Gennadas propinquus Rathbun

Gennadas propinquus Rathbun, 1906: 907, fig. 61.—Crosnier, 1978: 38, fig. 16b, 18d, e; Kensley, 1981b: 19.
Gennadas clavicarpus de Man, 1907: 144.—Kensley, 1971: 278, fig. 4; Griffiths & Brandt, 1983: 614.

Material examined. New Caledonia: AM P32910, east of New Caledonia, 21°05′E 166°45′E, 0–925 m, midwater trawl, *Kimbla* (K4/71-5), 9 May 1971; 6 specimens.

New South Wales: AM P32909, south-east of Port Jackson, 34°05′S 151°55′E to 34°10′S 152°14′E, 0–950 m, midwater trawl, *Kapala* (JP71-6), 25 Mar 1971; 1 specimen. AM P32904, south-east of Norah Head, 33°20′S 152°32′E to 33°24′S 152°31′E, 360 m, midwater

trawl, *Kapala* (K77-24-09), 14 Dec 1977; 8 specimens. AM P32902, north-east of Broken Bay, 33°27′S 152°30′E to 33°23′S 152°32′E, 630 m, midwater trawl, *Kapala* (K77-24-03), 13 Dec 1977; 3 specimens. AM P32901, north-east of Broken Bay, 33°31′S 152°20′E to 33°28′S 152°22′E, 569 m, midwater trawl, *Kapala* (K77-24-02), 12 Dec 1977; 1 specimen. AM P32906, north-east to east of Wollongong, 34°20′S 151°56′E to 34°25′S 151°54′E, 630 m, midwater trawl, *Kapala* (K77-24-12), 14 Dec 1977; 4 specimens. AM P32903, east of Norah Head, 33°17′S 52°31′E to 33°19′S 152°31′E, 90 m, midwater trawl, *Kapala* (K77-24-08), 13 Dec 1977; 6 specimens. AM P32905, north-east to east of Broken Bay, 33°28′S 152°34′E to 33°36′S 152°35′E, 630 m, midwater trawl, *Kapala* (K77-24-10), 14 Dec 1977; 1 specimen. AM P32900, east of Broken Bay, 33°33′S 152°18′E to 33°31′S 152°18′E, 216 m, midwater trawl, *Kapala* (K77-24-01), 12 Dec 1977; 2 specimens. AM P26594, north-east of Wollongong, 34°10′S 152°04′E to 34°12′S 152°02′E, 540 m, midwater trawl, *Kapala* (K77-18-01), 26 Oct 1977; 1 specimen. AM P32907, east to north-east of Norah Head, 33°20′S 153°04′E to 33°12′S 153°13′E, 630 m, midwater trawl, *Kapala* (K79-19-05), 28 Nov 1979; 1 specimen.

Diagnosis. Antennal angle of carapace acute, infra-antennal angle quadrate. Thelycum of female with W-shaped process on sternite 13 closely connected to bluntly triangular shield on sternite 12; sternite 14 with 8-shaped process. Petasma of male, external lobe bipartite, large median lobe of 2 diverging acute lobules, internal lobe of 2 rounded lobules, accessory lobe a simple rounded flap.

Remarks. Griffiths & Brandt (1983) record this species (as *G. clavicarpus)* associated with a warm-core eddy in the Tasman Sea off eastern Australia.

Distribution. Widespread through Indo-Pacific; surface to 1200 m.

Gennadas scutatus Bouvier

Gennadas scutatus Bouvier, 1906: 748.—Kensley, 1971: 288, fig. 10; Crosnier, 1978: 43, figs 17a, 19c; Griffiths & Brandt, 1983: 614.

Material examined. New Caledonia: AM P32911, east of New Caledonia, 21°05′S 166°45′E, 0–925 m, midwater trawl, *Kimbla* (K4/71-5), 9 May 1971; 3 specimens. AM P32912, east of New Caledonia, 22°03′S 167°44′E, 0–800 m, midwater trawl, *Kimbla* (K4/71-11), 13 May 1971; 1 specimen.

New South Wales: AM P32913, east of Norah Head, 33°17′S 152°31′E to 33°19′S 152°31′E, 90 m, midwater trawl, *Kapala* (K77-24-08), 13 Dec 1977; 1 specimen.

Diagnosis. Antennal and infra-antennal angles of carapace acute. Thelycum of female with sternite 12 triangular with seminal receptacles at base, sternite 13 triangular, sternite 14 with elongate flap extending forward over sternite 13 and reaching sternite 12. Petasma of male with external lobe of 2 rounded lobules, median lobe broad, of slender acute outer lobule and broadly truncate inner lobule; median lobe of 2 rounded lobules; accessory lobe a triangular flap.

Remarks. Griffiths & Brandt (1983) record this species associated with a warm-core eddy off eastern Australia.

Distribution. Caribbean; north-east and north-west Atlantic; west coast of South Africa; Indo-Pacific; surface to 600 m.

Gennadas tinayrei Bouvier

Gennadas tinayrei Bouvier, 1906: 10, figs 2–4, 14.—Kensley, 1971: 290, fig. 12; Crosnier, 1978: 44, figs 17b, 19d; Griffiths & Brandt, 1983: 614.

Material examined. New South Wales: AM P32888, north-east of Broken Bay, 33°31′S 152°20′E to 33°28′S 152°22′E, 569 m, midwater trawl, *Kapala* (K77-24-02), 12 Dec 1977; 1 specimen. AM P32890, east of Norah Head, 33°17′S 152°31′E to 33°19′S 152°31′E, 90 m, midwater trawl, *Kapala* (K77-24-08), 13 Dec 1977; 1 specimen. AM P32887, south-east of Norah Head, 33°20′S 152°32′E to 33°24′S 152°31′E, 360 m, midwater trawl, *Kapala* (K77-24-09), 14 Dec 1977; 2 specimens. AM P32891, north-east to east of Wollongong, 34°20′S 151°56′E to 34°25′S 151°54′E, 630 m, midwater trawl, *Kapala* (K77-24-12), 14 Dec 1977; 1 specimen.

Diagnosis. Antennal angle of carapace subacute, infra-antennal angle acute. Thelycum of female with narrow median posteriorly directed process on sternite 11; sternite 13 with broadly triangular process flanked by two rounded processes on each side; sternite 14 with small rectangular shield. Petasma of male with external lobe faintly divided into 2 apical lobules; median lobe broad, low, convex; inner lobe of 2 rounded lobules; accessory lobe bluntly rounded.

Remarks. Griffiths & Brandt (1983) found this species associated with a warm-core eddy off eastern Australia.

Distribution. North-east and north-west Atlantic; off west coast of South Africa; Indo-Pacific; 100–600 m.

Subfamily ARISTEINAE

Aristaeomorpha Wood Mason, 1891

Aristaeomorpha foliacea (Risso)

Penaeus foliaceus Risso, 1827: 69, pl. 2, fig. 6.
Aristaeomorpha foliacea.—Schmitt, 1926: 313, pl. 57, figs 1–3; Crosnier, 1978: 54, figs 23, 24; Grey, Dall & Baker, 1983: 36, pl. 1.

Material examined. New South Wales: AM P17966, east of Long Reef, 33°41–44′S 151°55–53′E, 540 m, bottom trawl, *Kapala* (K71-07-01), 20 April 1971; 1 specimen. AM P17904, north-east of Coffs Harbour, 29°51′S 153°40′E, 205 m, bottom trawl, *Kapala* (K71-09-03), 11 May 1971; 17 specimens. AM P18023, north-east to east of North Solitary Island, 29°49′S 153°42°E to 29°59′S 153°38′E, 369 m, demersal prawn trawl, *Kapala* (K71-09-04), 12 May 1971; 1 specimen. AM P18011, south-east of Gabo Island, 37°39′S 150°17′E to 37°42′S

150°17′E, prawn trawl, *Kapala* (K71-13-01), 30 July 1971; 3 specimens. AM P18017, P18022, P18016, south-east of Gabo Island, 37°45′S 150°13′E to 37°39′S 150°17′E, 405 m, trawl, *Kapala* (K71-13-02), 30 July 1971; 3 specimens. AM P18981, south-east to east of Broken Bay, 33°43′S 151°55′E to 33°37′S 152°02′E, 675 m, demersal prawn trawl, *Kapala* (K72-06-04), 19 Oct 1972; 3 specimens. AM P19155, east of Sydney, 33°00′S 151°43′E to 33°54′S 151°47′E, 732m, bottom trawl, *Kapala* (K72-07-01), 6 Nov 1972; 1 specimen. AM P19154, south-east of Broken Bay, 33°44′S 151°55′E to 33°40′S 151°58′E, 720 m, demersal prawn trawl, *Kapala* (K72-07-04), 9 Nov 1972; 1 specimen. AM P19002, north-east of Port Jackson, 33°52′S 151°50′E to 33°48′S 151°54′E, 765 m, demersal prawn trawl, *Kapala* (K72-07-15), 7 Dec 1972; 1 specimen. AM P19003, south-east of Broken Bay, 33°42′S 151°55′E to 33°40′S 151°57′E, 810 m, demersal prawn trawl, *Kapala* (K72-07-16), 7 Dec 1972; 9 specimens. AM P21048, P21043, north-east of Wollongong, 34°16′S 151°26′E to 34°22′S 151°23′E, 356 m, demersal prawn trawl, *Kapala* (K75-05-01), 8 Aug 1975; 3 specimens. AM P21036, north-east of Wollongong, 34°21′S 151°24′E to 34°14′S 151°28′E, 400 m, demersal prawn trawl, *Kapala* (K75-05-02), 8 Aug 1975; 2 specimens. AM P21011, east of Broken Bay, 33°27′S 152°03′E to 33°30′S 152°07′E, 540 m, trawl, *Kapala* (K75-05-04), 19 Aug 1975; 4 specimens. AM P25152, east of Broken Bay, 33°35′S 152°01′E to 33°32′S 152°03′E, 810 m, demersal prawn trawl, *Kapala* (K76-24-03), 20 Dec 1976; 1 specimen. AM P25371, south-east to east of Broken Bay, 33°34′S 151°52′E to 33°40′S 151°55′E, 405 m, demersal prawn trawl, *Kapala* (K77-12-01/02), 8 Aug 1977; 5 specimens. AM P26816, north-east of Norah Head, 33°08′S 152°27′E to 33°10′S 152°24′E, 580 m, demersal prawn trawl, *Kapala* (K77-23-09), 7 Dec 1977; 11 specimens. AM P33080, north-east of Point Danger, 28°01′S 154°00′E to 27°58′S 154°00′E, 542 m, demersal prawn trawl, *Kapala* (K78-17-10), 17 Aug 1978; 1 specimen. AM P33078, north-east of Point Danger, 28°03′S 154°04′E to 28°01′S 154°04′E, 724 m, demersal prawn trawl, *Kapala* (K78-23-08), 6 Nov 1978; 5 specimens. AM P33079, north-east of Norah Head, 33°08′S 152°27′E to 33°10′S 152°24′E, 580 m, demersal prawn trawl, *Kapala* (K77-23-09), 7 Dec 1977; 8 specimens. Victoria: AM P18011, south-east of Gabo Island, 37°39′S 150°17′E to 37°42′S 150°16′E, 387 m, Danish trawl, *Kapala* (K71-13-01), 30 July 1971; 3 specimens. AM P18017, P18022, P18016, south-east of Gabo Island, 37°39–45′S 150°17–13′E, 396-401 m, Danish trawl, *Kapala* (K71-13-02), 30 July 1971; 3 specimens.

Diagnosis. Body pubescent. Rostrum fairly long, reaching beyond scaphocerite in adult females and young males, shorter in adult males; up to 9 dorsal rostral spines, no ventral spines. Hepatic spine present. Thelycum of female with sternite 13 bearing anteriorly directed oval shield, sternite 14 bearing rounded medial process. Petasma in male roughly rectangular, with distolateral corner somewhat produced.

Distribution. Mediterranean; north-east and north-west Atlantic; Caribbean; Gulf of Mexico; Indo-West Pacific to Japan and Fiji; southern and eastern Australia; New Zealand; 90–1300 m.

Aristeus Duvernoy, 1840

Aristeus semidentatus Bate

Aristeus semidentatus Bate, 1881: 189.—Crosnier, 1978: 68, fig. 26g.

Material examined. New South Wales: AM P26772, south-east of Broken Bay, 33°40–35′S 151°56–58′E, 714–732 m, demersal prawn trawl, *Kapala* (K77-23-06), 6 Dec 1977; 1 ♀. AM P26777, south-east of Broken Bay, 33°40–35′S 151°56–58′E, 714–732 m, demersal prawn trawl, *Kapala* (K77-23-06), 6 Dec 1977; 1 ♂, 1 ♀. AM P25143, east of Broken Bay, 33°30–27′S 152°05–07′E, 810 m, demersal prawn trawl, *Kapala* (K76-24-04), 21 Dec 1976; 1 ♀. AM P33196, east of Broken Bay, 33°32′S 152°06′E to 33°34′S 152°05′E, 810 m, demersal prawn trawl, *Kapala* (K79-20-13), 6 Dec 1979; 1 ♂, 1 ♀. AM P33197, south-east of Broken Bay, 33°39′S 152°06′E to 33°37′S 152°07′E, 990 m, demersal prawn trawl, *Kapala* (K79-20-15), 6 Dec 1979; 2 ♀, 8 juvs.

Diagnosis. Carapace glabrous; branchiostegal spine produced posteriorly into supporting, anteriorly keeled ridge. Subdistal spine on external face of merus of pereopods 1 and 2. Fingers of pereopods relatively short. Photophores present on pereopods.

Remarks. Crosnier (1978) presented two tables in which characters of four species of *Aristeus* from Madagascar were compared. These features of *A. semidentatus* from Madagascar were compared with those for the present Australian material (see Tables 2 and 3). It was found that the number of photophores on the carpus and propodus of pereopods 1, 2, 4, and 5 was consistently lower than Crosnier's figures. Further, the ratio of chela to carpus in pereopod 1, and the ratio of carpus to merus in pereopod 5 was consistently higher than Crosnier's figures. For the remaining features provided in the diagnosis by Crosnier (1978: 68), the

		No. Photophores			No. Photophores
Prd 1	carpus	6—8	Prd 4	carpus	7—12
	propodus	2—3		propodus	8—11
	dactyl	0		dactyl	0
Prd 2	carpus	0—2	Prd 5	carpus	8—13
	propodus	1—2		propodus	8—13
	dactyl	0		dactyl	8—10
Prd 3	carpus	0—3			
	propodus	1—2			
	dactyl	0			

Table 2. Pereopodal photophore counts for Australian specimens of *Aristeus semidentatus*.

	chela/carpus			carpus/merus	
	Prd 1	Prd 2	Prd 3	Prd 4	Prd 5
♀	1.11—1.23	0.88—0.97	0.75—1.04	1.02—1.08	1.24—1.37
♂	1.12—1.15	0.92—0.94	0.78	1.02	1.40

Table 3. Pereopodal carpus/merus ratios for Australian specimens of *Aristeus semidentatus*.

Australian material is in agreement.

The present material may be differentiated from *A. mabahissae* by the lower ratio of chela/carpus of pereopod 1, and the higher ratio of carpus/merus of pereopod 5.

Aristeus virilis (Bate)

Hemipenaeus virilis Bate, 1881: 187.
Aristeus virilis.— Crosnier, 1978: 61, figs 25a, b, 26a, b.

Material examined. New South Wales: AM P21683, P21684, north-east of Wooli, 29°49′S 153°44′E, 503 m, prawn trawl, *Kapala* (K75-09-03), 10 Oct 1975; 12 specimens. AM P21684, south-east of Clarence River, 29°37′S 153°46′E, 410 m, demersal prawn trawl, *Kapala* (K75-09-04), 10 Oct 1975; ? specimens. AM P21686, north-east of Yamba, 29°26′S 153°49′E to 29°20′S 153°50′E, 450 m, demersal prawn trawl, *Kapala* (K75-09-08), 12 Oct 1975; 1 specimen. AM P24485, east of Sydney, 33°35′S 151°59′E, 366 m, *Kapala* (K76-09-02), 24 June 1976; 1 specimen. AM P26770, north-east of Norah Head, 33°11′S 152°24′E to 33°09′S 152°25′E, 720 m, demersal prawn trawl, *Kapala* (K77-23-10), 7 Dec 1977; 1 specimen. AM P33003, north-east of North Solitary Island, 29°53′S 153°42′E to 29°50′S 153°43′E, 453 m, demersal prawn trawl, *Kapala* (K78-06-07), 26 April 1978; 1 specimen. AM P33002, north-east of Point Danger, 28°03′S 154°04′E to 28°01′S 154°04′E, 724 m, demersal prawn trawl, *Kapala* (K78-23-08), 6 Nov 1978; 1 specimen.

Diagnosis. Body pubescent. Single movable subdistal spine present on external surface of merus of third pereopods. Between 16 and 22 photophores on propodus of pereopod 5. Thelycum in female with sternite 13 bearing broadly ovate, setose, anteroventrally-directed process. Petasma of male distally broad, somewhat produced mediodistally.

Distribution. Indo-West Pacific to New Caledonia, New Hebrides, and Japan; 400–900 m.

Plesiopenaeus Bate, 1881

Plesiopenaeus edwardsianus (Johnson)

Penaeus Edwardsianus Johnson, 1867: 897.
Plesiopenaeus edwardsianus.—Crosnier, 1978: 88, figs 31a–c, 32a–c, 33a; Grey, Dall & Baker, 1983: 38, pl. 2.

Material examined. New South Wales: AM 19103, 33°43–39′S 151°54–58′E, 694 m, *Kapala* (K72-05-01), 19 Oct 1972; 7 specimens. AM P19089, south-east to east of Broken Bay, 33°43′S 151°55′E to 33°37′S 152°02′E, 675 m, demersal prawn trawl, *Kapala* (K72-06-04), 19 Oct 1972; 6 specimens. AM P19090, east of Sydney, 34°00′S 151°43′E, 732 m, *Kapala* (K72-07-01), 6 Nov 1972; 1 specimen. AM P19102, east of Long Reef, 33°43–40′S 152°55–57′E, 823 m, *Kapala* (K72-17-12), 7 Dec 1972; 3 specimens. AM P20494, east of Broken Bay, 33°38–34′S 151°57′–152°01′E, 796 m, Kapala (K75-01-02), 2 April 1975; 2 specimens. AM P21005, P21006, east of Broken Bay, 33°32′S 152°04′E to 33°38′S 152°00′E, 810 m, demersal prawn trawl, *Kapala* (K75-05-05), 19 Aug 1975; 6 specimens. AM P25155, P25193, north-east of Broken Bay, 33°30′S 152°05′E to 33°27′S 152°07′E, 808 m, demersal prawn trawl, *Kapala* (K76-24-04), 21 Dec 1976; 25 specimens. AM P33084, south-east of Wollongong, 34°31′S 151°20′E to 34°34′S 151°19′E, 684 m, demersal prawn trawl, *Kapala* (K77-21-01), 21 Nov 1977; 2 specimens. AM P33085, south-east of Broken Bay, 33°40′S 151°56′E to 33°37′S 151°56′E, 711 m, demersal prawn trawl, *Kapala* (K77-23-06), 6 Dec 1977; 3 specimens. AM P26763, north-east of Norah Head, 33°11′S 152°24′E to 33°09′S 152°25′E, 720 m, demersal prawn trawl, *Kapala* (K77-23-10), 7 Dec 1977; 8 specimens. AM P33081, north-east of Danger Point, 28°03′S 154°04′E to 28°01′S 154°04′E, 724 m, demersal prawn trawl, *Kapala* (K78-23-08), 6 Nov 1978; 22 specimens. AM P33086, east of Broken Bay, 33°34′S 152°04′E to 33°31′S 152°06′E, 713 m, demersal prawn trawl, *Kapala* (K79-20-04), 4 Dec 1979; 1 specimen. AM P33083, off New South Wales, *Kapala* (K79-23); 3 specimens. AM P35917, east of Long Reef, 33°43–39′S 151°56–58′E, 630 m, demersal fish trawl, *Kapala* (K84-16-03), 25 Sept 1984; 1 specimen.

Diagnosis. Rostrum elongate, but becoming shorter in adult males, with 3 dorsal spines at base, ventral margin unarmed. Hepatic spine absent, postantennal spine absent. Podobranch present on pereopod 3. Epipodite on pereopod 4. Exopods lacking on pereopods. Abdominal segments 3–6 ending in small posterodorsal spine. Thelycum in female with small anteriorly directed spine on sternite 12; heart-shaped, anteriorly directed shield on sternite 13; roughly elongate rectangular shield on sternite 14. Scaphocerite of adult male modified, bearing slender distal prolongation.

Distribution. Widespread throughout the Indo-West Pacific and Atlantic Oceans; off New South Wales; 274–1850 m.

Family PENAEIDAE

Funchalia Johnson, 1867

Funchalia villosa (Bouvier)

Hemipenaeopsis villosus Bouvier, 1905: 981.
Funchalia villosa.—Dall, 1957: 163, fig. 9; Crosnier & Forest, 1973: 296; Casanova, 1976: 63; Casanova & Judkins, 1977: 125, 126; Kensley, 1977: 29, figs 8c, d; Crosnier, 1985: 869, figs 13a–e, 14b, c.

Material examined. New South Wales: AM P19464, north-east of Wollongong, 34°10′S 151°37′E to 34°14′S 151°35′E, 50 m, midwater trawl, *Kapala* (K73-01-01), 30 Apr 1973; 38 specimens. AM P32932, off Port Kembla, 34°28′S 151°29′E, 225 m, midwater trawl, *Kapala* (K74-05-JP1), 22 Jan 1974; 2 specimens. AM P26556, north-east of Batemans Bay, 35°36′S 150°55′E to 35°39′S 150°56′E, 540 m, midwater trawl, *Kapala* (K77-18-05), 27 Oct 1977; 1 specimen. AM P26557, north-east of Batemans Bay, 35°36′S 150°55′E to 35°39′S 150°56′E, 540 m, midwater trawl, *Kapala* (K77-18-05), 27 Oct 1977; 3 specimens. AM P30329, east of Broken Bay, 33°33′S 152°18′E to 33°31′S 152°18′E, 216 m, midwater trawl, *Kapala* (K77-24-01), 12 Dec 1977; 20 specimens. AM P32920, north-east of Broken Bay, 33°31′S 152°20′E to

33°28′S 152°22′E, 569 m, midwater trawl, *Kapala* (K77-24-02), 12 Dec 1977; 10 specimens. AM P32919, north-east of Broken Bay, 33°27′S 152°30′E to 33°23′S 152°32′E, 630 m, midwater trawl, *Kapala* (K77-24-03), 13 Dec 1977; 15 specimens. AM P32931, south-east of Norah Head, 33°23′S 152°27′E to 33°19′S 152°39′E, 666 m, midwater trawl, *Kapala* (K77-24-06), 13 Dec 1977; 1 specimen. AM P32929, north-east of Norah Head, 33°16′S 152°29′E to 33°14′S 152°30′E, 36 m, midwater trawl, *Kapala* (K77-24-07), 13 Dec 1977; 26 specimens. AM P32921, east of Norah Head, 33°17′S 152°31′E to 33°19′S 152°31′E, 90 m, midwater trawl, *Kapala* (K77-24-08), 13 Dec 1977; 27 specimens. AM P32922, south-east of Norah Head, 33°20′S 152°32′E to 33°24′S 152°31′E, 360 m, midwater trawl, *Kapala* (K77-24-09), 14 Dec 1977; 39 specimens. AM P32918, north-east to east of Broken Bay, 33°28′S 152°34′E to 33°36′S 152°35′E, 630 m, midwater trawl, *Kapala* (K77-24-10), 14 Dec 1977; 19 specimens. AM P32923, north-east of Wollongong, 34°05′S 152°02′E to 34°13′S 152°00′E, 630 m, midwater trawl, *Kapala* (K77-24-11), 14 Dec 1977; 17 specimens. AM P32924, north-east to east of Wollongong, 34°20′S 151°56′E to 34°25′S 151°54′E, 630 m, midwater trawl, *Kapala* (K77-24-12), 14 Dec 1977; 84 specimens. AM P32926, south-east of Newcastle, 33°03′S 152°58′E to 32°59′S 153°03′E, 482 m, midwater trawl, *Kapala* (K79-19-02), 27 Nov 1979; 6 specimens. AM P32925, north-east of Norah Head, 33°05′S 153°05′E to 33°13′S 153°05′E, 630 m, midwater trawl, *Kapala* (K79-19-03), 28 Nov 1979; 20 specimens. AM P32927, east of Newcastle, 32°59′S 153°03′E to 32°51′S 153°01′E, 391 m, midwater trawl, *Kapala* (K79-19-07), 29 Nov 1979; 3 specimens. AM P32928, north-east of Norah Head, 33°08′S 152°48′E to 33°16′S 152°46′E, 630 m, midwater trawl, *Kapala* (K79-19-10), 29 Nov 1979; 1 specimen.

Diagnosis. Rostrum with 4–5 dorsal teeth, ventrally unarmed. Carapace with 1 epigastric tooth; hepatic spine absent in adults; antennal spine present; branchiocardiac ridge prominent. Fifth and sixth abdominal somites with prominent lateral ridges. Petasma asymmetrical, shorter ramus distally a simple lobe with broad apical angle; longer ramus distally deeply grooved and curved, with pair of blunt lateral knobs distally, blunt triangular projection on outer proximal margin. Thelycum forming deep receptacle, anterior plate between pereopod 4 bases cordiform, grooved, lateral edges curved ventrally, anteriorly acute; sternal plate roughly quadrangular, with anterolateral extensions fusing with anterior plate to form walls of seminal receptacle.

Distribution. Eastern and western Atlantic, Mediterranean, Caribbean, south-western Indian Ocean, off Lord Howe Island; 50–666 m.

Funchalia woodwardi Johnson

Funchalia Woodwardi Johnson, 1867: 895
Funchalia woodwardi.—Crosnier & Forest, 1973: 296; Casanova, 1976: 64; Casanova & Judkins, 1977: 125; Kensley, 1977: 29, fig. 8A, B.

Material examined. New South Wales: AM P26555, north-east of Batemans Bay, 35°36′S 150°55′E to 35°39′S 150°56′E, 540 m, midwater trawl, *Kapala* (K77-18-05), 27 Oct 1977; 1 ♀.

Diagnosis. Rostrum with 10–12 dorsal teeth, ventrally Eral ridges. Petasma asymmetrical, shorter ramus distally a simple lobe with broad apical angle; longer ramus distally deeply grooved and curved, with pair of blunt lateral knobs distally, blunt triangular projection on outer proximal margin. Thelycum forming deep receptacle, anterior plate between pereopod 4 bases cordiform, grooved, lateral edges curved ventrally, anteriorly acute; sternal plate roughly quadrangular, with anterolateral extensions fusing with anterior plate to form walls of seminal receptacle.

Distribution. North-eastern Atlantic, Mediterranean, south-eastern South Africa; 250–540 m.

Parapenaeus Smith, 1885

Parapenaeus sextuberculatus Kubo

Parapenaeus sextuberculatus Kubo, 1949: 403, figs 7F, 21B, 28D–F, 47R, 61A,A′, 75B,H, 78H, 143B,F.—Dall, 1957: 179; Hall, 1962: 31; Crosnier, 1985: 312, 330, figs 9a,d, 10a-c, 11a.

Material examined. New South Wales: AM P32469, south-east of Coffs Harbour, 30°20′S 153°16′E to 30°23′S 153°25′E, 279 m, demersal prawn trawl, *Kapala* (K77-13-05), 19 Aug 1977; 1 ♂. AM P32484, east of Brooms Head, 29°44–50′S 153°41–39′E, 162 m, trawl, *Kapala* (K78-21-10), 11 Oct 1978; 7 ♀. AM P32485, east of Brooms Head, 29°36–40′S 153°45–43′E, 270 m, trawl, *Kapala* (K78-06-04), 26 Apr 1978; 1 ♂. AM P32486, east of Sugarloaf Point, 32°06–03′S 153°04–05′E, 360 m, prawn trawl, *Kapala* (K77-13-01), 17 Aug 1977; 1 ♂, 1 ♀. AM P32487, east of Port Jackson, 33°53′S 151°50′E, 360 m, *Kapala* (K77-09-02), 4 July 1977; 2 ♀. AM P32489, east of Brooms Head, 29°47–49′S 153°41–40′E, 234 m, *Kapala* (K78-05-07), 19 Apr 1978; 3 ♂, 4 ♀. AM P32490, east of Brooms Head, 29°47–49′S 153°41–40′E, 234 m, *Kapala* (K78-05-07), 19 Apr 1978; 1 ♀.

Diagnosis. Rostrum very slightly arched, with 5–6 dorsal teeth, well separated from epigastric tooth. Branchiostegal spine present, situated on anterior carapace margin. Abdominal somite 6 less than twice length of somite 5. Thelycum with plate of sternite XIII having cordiform anteriorly directed process; sternite XIV with pair of anteriolateral somewhat transversely elongate tubercles, pair of rounded posterolateral tubercles, single low rounded posteromedian tubercle. Petasma distally broadly rounded and with small distal point, distolateral plate distally bifid and with rounded anterior and posterior ridges.

Distribution. Japan, Philippines, Indonesia, India, 140–320 m; Madagascar, 250–350 m.

Penaeopsis Bate, 1881

Penaeopsis eduardoi Pérez Farfante

Penaeopsis eduardoi Pérez Farfante, 1977b: 172, figs 1–4.

Material examined. New South Wales: AM P32462, east of Port Jackson, 33°46′S 151°49′E to 33°44′S 151°51′E, 425 m, trawl, *Kapala* (K80-21-01), 16 Dec 1980; 2 ♀. AM P32463, north-east of Danger Point, 29°53′S 153°42′E to 29°55′S 153°42′E, 405 m, trawl, *Kapala* (K78-06-06), 26 Apr 1978; 5 ♀. AM P32464, north-east of Danger Point, 27°55′S 154°03′E to 27°57′S 154°03′E, 540 m, trawl, *Kapala* (K78-23-09), 6 Nov 1978; 1 ♂, 3 ♀. AM P32465, east of Broken Bay, 33°27—30′S 151°05—03′E, 391 m, prawn trawl, *Kapala* (K79-12-07), 21 Aug 1979; 1 ♂. AM P32466, south-east of Cape Byron, 28°41′S 153°51′E to 28°44′S 153°52′E, 149 m, demersal prawn trawl, *Kapala* (K78-17-21), 18 Aug 1978; 1 ♂. AM P32467, off Sydney, 33°46′S 151°50′E to 33°42′S 151°53′E, 414 m, demersal prawn trawl, *Kapala* (K80-06-01), 24 May 1980; 1 ♂. AM P32468, north-east of Danger Point, 27°55′S 154°03′E to 27°57S 154°03′E, 629 m, demersal prawn trawl, *Kapala* (K78-23-09), 6 Nov 1978; 1 ♂. AM P32470, east of Long Reef, 33°42—39′S 151°52—54′E, 447 m, prawn trawl, *Kapala* (K74-24-01), 20 Dec 1976; 1 ♂. AM P32474, north-east of Danger Point, 28°01′S 154°00′E to 27°58′S 154°00′E, 542 m, demersal prawn trawl, *Kapala* (K78-17-10), 17 Aug 1978; 1 ♀. AM P32493, east of Sugarloaf Point, 32°19—16′S 153°00—02′E, 360 m, trawl, *Kapala* (K78-03-03), 5 Apr 1978; 4 ♀.

Diagnosis. Rostrum horizontal to slightly upturned, with 8—15 dorsal teeth; epigastric tooth well separated from rostral teeth. Telson bearing 2 pairs of articulated lateral spines; terminally hastate. Thelycum with plate of sternite XIV with caudally pedunculate posteromedian tubercle; sternite XIII with plate caudally bifid; sternite of XII basally broad, conical, directed anteriorly. Petasma with ventral costa produced into distal spine projecting well beyond cincinnuli.

Distribution. Bay of Bengal to Japan, Philippines, Indonesia, Taiwan, Fiji; 290—570 m.

Penaeus Fabricius, 1798

Penaeus longistylis Kubo

Penaeus longistylis Kubo, 1943: 200.—1949: 282, figs 7A, 24F,G, 49I, 58E, 73C,I, 77Q, 109—111; Hall, 1962: 15, fig. 81; Racek & Dall, 1965: 13, pl. 1, fig. 2; Grey, Dall & Baker, 1983: 50, pl. 8.
Penaeus jejunus Hall, 1956: 75; 1962: 16.
Penaeus caesius Dall, 1957: 143, fig. 2A-G.

Material examined. New South Wales: AM P33165, south-east of Coffs Harbour, 30°20′S 153°16′E to 30°23′S 53°25′E, 270 m, demersal prawn trawl, *Kapala* (K77-13-05), 19 Aug 1977; 1 ♀. AM P33166, south-east of Cape Hawke, 32°18′S 152°43′E to 32°12′S 152°43′E, 90 m, demersal prawn trawl, *Kapala* (K78-19-06), 12 Sept 1978; 2 ♂, 1 ♀. AM P33164, north-east of North Solitary Island, 29°44′S 153°41′E to 29°50′S 153°39′E, 160 m, demersal prawn trawl, *Kapala* (K78-21-10), 10 Oct 1978; 1 ♀.

Diagnosis. Rostrum with 12 dorsal teeth, single anteroventral tooth. Adrostral groove almost reaching posterior margin of carapace; median groove of postrostral carina much less than half length of carapace; hepatic carina and gastro-frontal carina well developed. Stylocerite reaching or just falling short of distal end of basal antennular peduncle article. Pereopod 1 with stout ischial spine. Petasma with median lobe apically rounded, reaching as far as distal margin of lateral lobe. Thelycum with anterior plate anteriorly elongate, apically narrowly rounded; posterior plate between bases of pereopod 5 consisting of 2 plates meeting in midline, together forming broadly oval structure.

Infraorder CARIDAE

Family OPLOPHORIDAE

Acanthephyra A. Milne Edwards, 1881

Acanthephyra acutifrons Bate

Acanthephyra acutifrons Bate, 1888: 749, pl. 126 fig. 3.—Chace, 1940: 146—147, fig. 23; Holthuis, 1951: 28; Crosnier & Forest, 1973: 28, fig. 8b.

Material examined. New South Wales: AM P26836, 70 km east of Broken Bay, 33°29′S 152°25′E to 33°23′S 152°28′E, 0—630 m, midwater trawl, J.R.Paxton, *Kapala* (K77-24-03), 13 Dec 1977; 1 specimen.

Diagnosis. Rostrum less than half carapace length, basally deep, 1 ventral spine; carapace dorsally carinate, denticulate anteriorly, carina behind branchiostegal spine very short; all abdominal segments carinate, segments 3—6 with a dorsal terminal spine; telson with 5—6 pairs of dorsolateral spinules.

Remarks. *Acanthephyra acutifrons* is the largest of the species of this genus collected off eastern Australia in this survey. This specimen is similar in size to the ovigerous female figured by Chace (1940). The denticles behind the rostrum are much less prominent than in the smaller specimen figured by Crosnier & Forest (1973). The sixth abdominal segment is short, dorsal length less than 1.5 times the posterior height.

This species is distinguished from the similar, but much smaller, *A. curtirostris* by the presence of a carina on the first abdominal segment, the very short carina behind the branchiostegal spine, the short sixth abdominal segment and the smaller number of dorsolateral spinules on the telson.

This species has not previously been recorded off eastern Australia.

Distribution. Indo-west Pacific, eastern and western Atlantic; 650—2400 m.

Acanthephyra curtirostris Wood-Mason

Acanthephyra acutifrons Bate, 1888: 749 (in part, see Kemp, 1906).
Acanthephyra curtirostris Wood-Mason **in** Wood-Mason & Alcock, 1891: 195.—1892: 364—365, fig. 5; Kemp, 1906: 22, 24; Chace, 1940: 143—144, fig. 21; Crosnier & Forest, 1973: 39—41, fig. 8a; Kensley, 1981a: 57; 1981b: 21.

Material examined. New Caledonia: AM P32863, 22°03′S 167°44′E, 0—800 m, midwater trawl, *Kimbla* (K4/71-11), 13 May 1971; 1 ovig. ♀.

New South Wales: AM P26837, 70 km east of Broken Bay, 33°29′S 152°25′E to 33°23′S 152°28′E, 0—630 m, midwater trawl, *Kapala* (K77-24-03), 13 Dec 1977; 1 specimen.

Diagnosis. Rostrum less than half carapace length, basally deep, 1 ventral spine. Carapace dorsally carinate, carina behind branchiostegal spine about ⅓ carapace length; first abdominal segment not carinate; segments 3—6 carinate with dorsal, terminal spine; telson with 8—9 pairs of dorsolateral spinules.

Remarks. *Acanthephyra curtirostris* is similar to *A. acutifrons* in having a short rostrum with one ventral spine. It is distinguished from that larger species by the presence of a longer carina behind the branchiostegal spine, the absence of a dorsal carina on the first abdominal segment, the presence of 8—9 pairs of dorsolateral spinules on the telson and a longer sixth abdominal segment in which the dorsal length is more than twice the posterior height.

Distribution. Indo-west Pacific, northeastern Atlantic, Caribbean; 630—4970 m.

Acanthephyra pelagica (Risso)

Pandalus pelagicus Risso, 1816: 79

Acanthephyra pelagica.—Holthuis, 1947: 315—316; Kensley, 1972: 40 (in key), fig. 18E, F; 1981a: 57; 1981b: 21; Crosnier & Forest, 1973: 29—31.

Material examined. New South Wales: AM P32853, 70 km east of Tuggerah Lake, 33°19′S 152°25′E to 33°23′S 152°28′E, 0—630 m, midwater trawl, *Kapala* (K77-24-03), 13 Dec 1977; 1 specimen. AM P32854, 80 km east of Tuggerah Lake, 33°20′S 152°32′E to 33°24′S 152°31′E, 0—360 m, midwater trawl, *Kapala* (K77-24-09), 14 Dec 1977; 1 specimen. AM P32855, 65 km east of Broken Bay, 33°31′S 152°20′E to 33°28′S 152°22′E, 0—540 m, midwater trawl, *Kapala* (K77-24-02), 12 Dec 1977; 1 specimen. AM P26606, south-east of Port Hacking, 34°10′S 150°04′E to 34°12′S 150°02′E, 0—660 m, midwater trawl, *Kapala* (K77-18-01), 26 Oct 1977; 1 specimen. AM P32856, 80 km east of Lake Illawarra, 34°20′S 151°56′E to 34°25′S 151°54′E, 0—630 m, midwater trawl, *Kapala* (K77-24-12), 14 Dec 1977; 4 specimens. AM P32857, off Lake Illawarra, 34°40′S 151°15′E to 34°35′S 151°17′E, 594—675 m, fish trawl, *Kapala* (K77-19-05), 3 Nov 1977; 1 specimen. AM P26607, east of Brush Island, 35°36′S 150°55′E to 35°39′S 150°52′E, 0—650 m midwater trawl, *Kapala* (K77-18-05), 27 Oct 1977; 1 specimen.

Diagnosis. Rostrum more than half carapace length with evenly spaced spines on dorsal and ventral margins. No carina running entire length of carapace; first abdominal segment not carinate, segments 3—6 carinate with dorsal terminal spine; telson with 7—11 pairs of dorsolateral spinules.

Remarks. This species is distinguished from the more common *A. quadrispinosa* by the presence of 7—11 rather than four dorsolateral spinules on the telson.

These specimens were collected from 33°20′S to 35°40′S in trawls to a depth of 675 m.

Distribution. Indo-Pacific, north and south Atlantic, Mediterranean; 540—2166 m.

Acanthephyra quadrispinosa Kemp

Acanthephyra quadrispinosa Kemp, 1939: 576.—Kensley, 1968: 311; 1972: 40 (in key), fig. 18C, D; 1981a: 57; 1981b: 21.

Material examined. New Caledonia: AM P32832, 19°55′S 170°00′E, 0—500 m, midwater trawl, *Kimbla* (K4/71-8), 12 May 1971; 8 specimens. AM P32833, 21°05′S 166°45′E, 0—925 m, midwater trawl, *Kimbla* (K4/71-5), 9 May 1971; 2 specimens. AM P32834, 22°03′S 167°44′E, 0—800 m, midwater trawl, *Kimbla* (K4/71-11), 13 May 1971; 3 specimens.

New South Wales: AM P32841, off Port Stephens, 32°59′S 153°03′E to 32°51′S 153°01′E, 495 m, midwater trawl, *Kapala* (K75-19-07), 29 Nov 1979; 4 specimens (1 ovig. ♀). AM P32842, off Newcastle, 33°05′S 153°05′E to 33°13′S 153°05′E, 630 m, midwater trawl *Kapala* (K79-19-03), 28 Nov 1979; 43 specimens. AM P32849, off Newcastle, 33°03′S 152°58′E to 32°59′S 153°03′E, 630 m, midwater trawl, *Kapala* (K79-19-02), 27 Nov 1979; 3 specimens. AM P32850, off Newcastle, 33°07′S 153°11′E to 33°01′S 153°05′E, 630 m, midwater trawl, *Kapala* (K79-19-06), 28 Nov 1979; 2 specimens. AM P32846, off Norah Head, 33°15′S 153°06′E to 33°20′S 153°04′E, 360 m midwater trawl, *Kapala* (K79-19-04), 28 Nov 1979; 1 specimen. AM P32847, off Norah Head, 33°20′S 153°04′E to 33°12′S 153°13′E, 630 m, midwater trawl, *Kapala* (K79-19-05), 28 Nov 1979; 2 specimens. AM P32839, 80 km east of Tuggerah Lake, 33°20′S 152°32′E to 33°24′S 152°31′E, 0—360 m, midwater trawl, *Kapala* (K77-24-09), 14 Dec 1977; 57 specimens (1 ovig. ♀). AM P32848, 70 km east of Broken Bay, 33°19′S 152°25′E to 33°23′S 152°28′E, 0—630 m, midwater trawl, *Kapala* (K77-24-03), 13 Dec 1977; 29 specimens (1 ovig. ♀). AM P32843, 100 km east of Broken Bay, 33°28′S 152°34′E to 33°36′S 152°35′E, 0—630 m, midwater trawl, *Kapala* (K77-24-10), 14 Dec 1977; 122 specimens (8 ovig. ♀). AM P32851, 65 km east of Broken Bay, 33°31′S 152°20′E to 33°28′S 152°22′E, 0—540 m, midwater trawl, *Kapala* (K77-24-02), 12 Dec 1977; 8 specimens. AM P32844, 65 km east of Sydney Heads, 34°05′S 152°02′E to 34°13′S 152°00′E, 0—630 m, midwater trawl, *Kapala* (K77-24-11), 14 Dec 1977; 41 specimens (2 ovig. ♀). AM P32835, south-east of Sydney, 34°02′S 152°12′E to 34°14′S 152°14′E, 0—600 m, midwater trawl, *Kapala* (JP71-8), 25—26 Mar 1971; 19 specimens (2 ovig. ♀). AM P32836, south-east of Sydney, 34°05′S 151°55′E to 34°10′S 152°14′E, 0—950 m, midwater trawl, *Kapala* (JP71-6), 25 Mar 1971; 126 specimens (11 ovig. ♀). AM P32837, south-east of Sydney, 34°05′S 151°56′E to 34°09′S 152°05′E, 0—1200 m, midwater trawl, *Kapala* (JP71-1), 23 Mar 1971; 4 specimens (1 ovig. ♀). AM P32838, south-east of Sydney, 34°09′S 152°07′E to 34°14′S, 152°14′E, 0—250 m, midwater trawl, *Kapala* (JP71-4), 24—25 Mar 1971; 102 specimens (1 ovig. ♀). AM P26605, P26599, south-east of Port Hacking, 34°10′S 152°04′E to 34°12′S 152°02′E, 0—660 m, midwater trawl, *Kapala* (K77-18-01), 26 Oct

1977; 12 specimens (1 ovig. ♀). AM P32845, 80 km east of Lake Illawarra, 34°20′S 151°56′E to 34°25′S 151°54′E, 0—630 m, midwater trawl, *Kapala* (K77-24-12), 14 Dec 1977; 14 specimens. AM P32852, off Lake Illawarra, 34°40′S 151°15′E to 34°35′S 151°17′E, 594—675 m, fish trawl, *Kapala* (K77-19-05), 3 Nov 1977; 17 specimens. AM P24773, east of Brush Island, 35°28′S 150°50′E to 35°33′S 150°47′E, 567—594 m, fish trawl, *Kapala* (K76-11-12), 8 July 1976; 1 specimen. AM P26562, P26563, east of Brush Island, 35°36′S 150°55′E to 35°39′S 150°52′E, 0—650 m, midwater trawl, *Kapala* (K77-18-05), 27 Oct 1977; 22 specimens. AM P32840, east of Cape Howe, 37°24′S 150°30′E to 37°28′S 150° 33′E, 0—540 m, fish trawl, *Kapala* (K77-19-03), 1 Nov 1977; 6 specimens.

Diagnosis. Rostrum more than half carapace length with evenly spaced spines on dorsal and ventral margins. No carina running entire length of carapace; first abdominal segment not carinate, segments 3—6 carinate with a dorsal terminal spine; telson with 4 pairs of dorsolateral spinules.

Remarks. *Acanthephyra quadrispinosa* was by far the most commonly caught species of *Acanthephyra.* Specimens were collected from 20°S to 22°S, off New Caledonia, in trawls to a depth of 925 m, and from 33°S to 37°30′S off New South Wales, in trawls to a depth of 1200 m.

Colour. Colour in life uniformly bright red.

Distribution. Indo-Pacific, south Atlantic; 250—1700 m.

Acanthephyra smithii Kemp

Acanthephyra smithii Kemp, 1939: 572—573, 577—578.—Hayashi & Miyake, 1969: 61—63, fig. 2.

Material examined. New Caledonia: AM P32858, 19°55′S 170°E, 0—550 m, midwater trawl, *Kimbla* (K4/71-8), 12 May 1971; 3 specimens. AM P32859, 22°03′S 167°44′E, 0—800 m, midwater trawl, *Kimbla* (K4/71-11), 13 May 1971; 1 specimen.

New South Wales: AM P32860, 100 km east of Broken Bay, 33°28′S 152°34′E to 33°36′S 152°35′E, 0—630 m, midwater trawl, *Kapala* (K77-24-10), 14 Dec 1977; 1 specimen. AM P32861, 70 km east of Broken Bay, 33°33′S 152°18′E to 33°35′S 152°17′E, 0—216 m, midwater trawl, *Kapala* (K77-24-01), 12 Dec 1977; 2 specimens. AM P32862, 65 km east of Sydney Heads, 34°05′S 152°02′E to 34°13′S 152°OO′E, 0—630 m, midwater trawl, *Kapala* (K77-24-11), 14 Dec 1977; 2 specimens (2 ovig. ♀).

Diagnosis. Rostrum more than half carapace length with evenly spaced spines on dorsal and ventral margins. Carina running entire length of carapace; first abdominal segment not carinate, a medial V-shaped indentation on posterior margin; segments 3—6 carinate with dorsal, terminal spine; telson with 4 pairs of dorsolateral spinules.

Remarks. In this species the carinae on abdominal segments 2—6 are high and end in a strong spine on segments 3—6; the pleura of the fourth and fifth abdominal segments are similar in shape and the sixth abdominal segment is short, the dorsal length is about 1.5 times the posterior height. In *A. quadrispinosa* and *A. pelagica* there is no medial V-shaped indentation on the posterior margin of the first abdominal segment; on the fifth abdominal segment the posterolateral angle of the pleura is more strongly produced backwards than it is on the fourth segment and the dorsal length of the sixth segment is more than twice the posterior height.

These specimens were collected from 20°S to 34°S in trawls to a depth of 800 m.

Acanthephyra smithii has not previously been recorded from eastern Australian waters or further south than 24°S.

Distribution. Indian Ocean, western to central Pacific; 216—800 m.

Janicella Chace, 1986

Janicella spinicauda (A. Milne Edwards)

Oplophorus spinicauda A. Milne Edwards, 1883, pl. 30.—Chace, 1940: 184—186, fig. 54; Hayashi & Miyake, 1969: 68—69; Kensley, 1972: 38 (in key), figs 17D,E; 1981a: 58; 1981b: 22.

Janicella spinicauda.—Chace, 1986: 44, figs 23, 24.

Material examined. New Caledonia: AM P32864, 21°05′S 166°45′E, 0—925 m, midwater trawl, *Kimbla* (K4/71-5), 9 May 1971; 1 ovig. ♀.

Diagnosis. Rostrum about twice carapace length, with spines on dorsal and ventral margins. Lateral margin of scaphocerite with 3 well spaced teeth in distal half. Third maxillipeds and first pereopods with foliaceous exopods. Only abdominal segments 2—4 carinate, each with prominent terminal dorsal spine. Telson with long spine on either side of base of setose terminal appendage.

Remarks. This species is distinguished from others in the genus by the presence of a strong terminal spine on the second abdominal segment and the form of the telson.

Our only specimen was collected off New Caledonia; *J. spinicauda* has not been recorded off New South Wales.

Distribution. Indo-Pacific, north and south Atlantic; 460—1120 m.

Meningodora Smith, 1882

Meningodora mollis Smith

Meningodora mollis Smith, 1882: 74, pl. 11, figs 8, 9, pl. 12, figs 5—9.—Kensley, 1972: 36 (in key), fig. 16I; Crosnier & Forest, 1973: 44—46, fig. 10c.

Material examined. New Caledonia: AM P33138, 21°05′S 166°45′E, 0—925 m, midwater trawl, *Kimbla* (K4/71-5), 9 May 1971; 2 specimens.

Diagnosis. Rostrum short, not exceeding or only slightly exceeding eyes, with about 7 dorsal teeth, no ventral teeth; eyes slightly narrower than the eyestalk.

Dorsal margin of carapace carinate, without teeth in posterior three-quarters; only 1 lateral carina running entire length of carapace; first abdominal segment noncarinate; third segment without terminal dorsal spine or lobe; fourth to sixth segments carinate, with terminal dorsal spine.

Remarks. In these specimens the cornea is only slightly narrower than the eyes-stalk, i.e., they agree with the specimen figured by Crosnier & Forest (1973). The third abdominal segment is carinate dorsally and the propod of the third pereopod is 2.5 times as long as the dactyl. The short rostrum and the narrow cornea distinguish this species from *M. vesca.*

Distribution. Western and eastern Atlantic, Indian Ocean, western and eastern Pacific; 840—2160 m.

Meningodora vesca (Smith)

Notostomus viscus Smith, 1886: 189, 192 (nomen nudum).
Notostomus vescus.—Chace, 1940: 153—156, figs 29, 30.
Meningodora vesca.—Crosnier & Forest, 1973: 46—48, fig. 10d; Kensley, 1981b: 22.

Material examined. New Caledonia: AM P33139, 22°03′S 167°44′E, 0—800 m, midwater trawl, *Kimbla* (K4/71-11), 13 May 1971; 3 specimens.

New South Wales: AM P33140, 100 km east of Broken Bay, 33°28′S 152°34′E to 33°36′S 152°35′E, 0—630 m, midwater trawl, *Kapala* (K77-24-10), 14 Dec 1977; 1 specimen. AM P19097, off Sydney, 34°05′S 151°55′E to 34°10′E 152°14′E, 0—about 950 m, midwater trawl, *Kapala* (JP71-6), 25 Mar 1971; 3 specimens. AM P26603, north-east of Cape Howe, 37°24′S 150°30′S to 37°28′S 150°33′E, 0—540 m, midwater trawl, *Kapala* (K77-19-03), 1 Nov 1977; 2 specimens.

Diagnosis. Rostrum about ⅓ carapace length, with about 9—12 dorsal teeth and usually 1 or 2 ventral teeth. Cornea wider than eyestalk. Dorsal margin of carapace carinate, without teeth in posterior three-quarters; only 1 lateral carina running entire length of carapace; first abdominal segment not carinate; third segment without terminal dorsal spine or lobe; fourth to sixth segments carinate with a terminal dorsal spine.

Remarks. This species is distinguished from *M. mollis* by the longer rostrum and the larger cornea of the eye.

The specimens from off New South Wales were collected between 33°28′S and 37°28S′ in trawls at depths to 950 m.

Distribution. South-western and south-eastern Atlantic, Indo-west Pacific; 615—5400 m.

Notostomus A. Milne Edwards, 1881

Notostomus cf. *crosnieri* MacPherson

Notostomus crosnieri MacPherson, 1984: 54, figs 6a, 7a, 8a,b.
Notostomus auriculatus Barnard, 1950: 670, figs 124h, i.—Crosnier & Forest, 1973: 52—56, figs 14, 16c.
Notostomus sp. Holthuis & Sivertsen, 1967: 32—36, figs 4, 5.

Material examined. New South Wales: AM P33146, east of Port Stephens, 32°59′S 153°03′E to 32°51′S 153°01′E, 495 m, midwater trawl, *Kapala* (K79-19-07), 29 Nov 1979; 7 specimens (6 ovig. ♀). AM P33147, 70 km east of Broken Bay, 33°25′S 152°31′E, 0—630 m, midwater trawl, *Kapala* (K77-24-03), 13 Dec 1977; 1 specimen. AM P33148, 100 km east of Broken Bay, 33°28′S 152°33′E, 0—630 m, midwater trawl, *Kapala* (K77-24-10), 14 Dec 1977; 4 specimens (1 ovig. ♀). AM P33149, south-east of Sydney, 34°05′S 151°55′E to 34°10′S 152°14′E, 0—about 95O m, midwater trawl, *Kapala* (JP71-6), 25 Mar 1971; 1 specimen. AM P26564, P26565, east of Brush Island, 35°36′S 150°55′E to 35°39′S 150°52′E, 0—650 m, midwater trawl, *Kapala* (K77-18-05), 27 Oct 1977; 2 specimens. AM P35915, east of Long Reef, 33°43′S 151°56′E to 33°39′S 151°58′E, 626—637 m, demersal fish trawl, *Kapala* (K84-16-03), 25 Sept 1984; 1 juv.

Diagnosis. Dorsal carina of carapace finely denticulate along whole length; 5 lateral carinae on posterior carapace. All abdominal segments carinate, segments 3—6 with a terminal medial spine. Upper lateral rostral carina extending behind the orbital margin; lower lateral rostral carina not continuous with gastro-orbital carina; gastro-orbital carina with anterior extremity produced laterally, appearing as an obtuse angle in dorsal view. Stylocerite reaching at least midlength of third segment of antennular peduncle.

Remarks. These specimens agree with the figure of the carapace of the type of *N. auriculatus* given by Barnard (1950). They also agree with the description and figures of incomplete specimens, from an albatross chick, given by Holthuis & Sivertsen (1967). In most respects they agree with the specimens figured and described as *N. auriculatus* by Crosnier & Forest (1973), but described as a new species, *N. crosnieri,* by MacPherson (1984).

The dorsal carina is as figured by Crosnier & Forest with an abrupt slope to the posterior carapace margin, anteriorly with the denticles changing to quite large teeth above the orbit. The upper lateral rostral carina extends posteriorly beyond the margin of the orbit and curves slightly ventrally; both upper and lower lateral carinae continue forwards onto the rostrum and are quite distinctly visible along at least two-thirds of its length. The anterior extremity of the gastro-orbital carina, in all our specimens, is produced into a rounded lobe, very clearly visible in dorsal view. This lobe was described and figured by Holthuis & Sivertsen and appears also to be shown in the figure given by Barnard. Crosnier & Forest (1973) do not say whether such a lobe was present on their specimens. On all our specimens the subhepatic and infrahepatic carinae meet posteriorly as shown in Barnard's figure rather than remaining separate as shown by Crosnier & Forest (1973) and MacPherson (1984, Fig. 7B).

The first abdominal segment is strongly indented medially on the posterior margin and the length of the dorsal carina is about half (i.e. 0.42—0.58) the length of the segment at its articulation with the second segment. This is still clearly less than the same measurement in *N. elegans* but greater than the 0.25—0.4 of Crosnier & Forest's specimens of *P. auriculatus;* further, the carina also lacks the small anterior spine present in Crosnier & Forest's specimens, and figured by MacPherson (1984, Fig. 8B).

The dorsal carina of the second abdominal segment is subequal (0.9—1.0) to the length of the segment at its articulation with the first segment, but there is no posterior spine on the carina as in Crosnier & Forest's specimens. The lengths of the pereopods agree with that given by Crosnier & Forest for their specimens. The carpus of pereopods 3 and 4 is more than one-third the length of the propod in the adult, the dactyl slightly more than one-quarter the length of the propod (see Table 4).

	cl 21.3 mm	cl 46.5 mm
Pereopod 3		
carpus/propod	0.34	0.39
dactyl/propod	0.28	0.28
Pereopod 4		
carpus/propod	0.32	0.38
dactyl/propod	0.28	0.26

Table 4. Pereopodal ratios for two specimens of *Notostomus* cf. *crosnieri.*

There are four to six pairs of dorsolateral spinules on the telson, rather than the three pairs in Crosnier & Forest's specimens.

The differences between our specimens from eastern Australia and those of Crosnier & Forest, and MacPherson from the Atlantic may only indicate geographic variability in a very widely occurring species. However, the differences are of an order used to distinguish other species from one another. It is possible, especially regarding the large number of specimens available to us and to Crosnier & Forest, and MacPherson, that the Australian material is a separate species (see Table 5).

These specimens can be distinguished from specimens of *N. elegans* using the characters of the upper lateral rostral carina teeth at the base of the rostrum, stylocerite, and first abdominal segment given by Crosnier & Forest (1973). We would add the presence of an anterior lobe on the gastro-orbital carina of *N. crosnieri.* Also, *N. crosnieri* lacks the carinae on the pleura of the abdominal segments present in *N. elegans.* On the third to fifth segment there is an oblique groove on the anterior part of the pleuron (shown in Crosnier & Forest, 1973, fig. 14) rather than the curved carina in *N. elegans.* Differences between the two species are also discussed under *N. elegans.*

These specimens were trawled at depths up to 900 m between 32°50′S and 35°40′S.

Colour. Colour in life of *N.* cf. *crosnieri* is uniformly bright red.

Distribution. Western and southern coasts of Africa, Tristan da Cunha, eastern Australia, south-eastern Pacific.

	N. crosnieri specimens	Eastern Australian specimens
rostral carinae	on basal 1/3 of rostrum	on 2/3 to 3/4 of rostrum
anterior of gastro-orbital carina	? produced	obtuse lobe
subhepatic & infrasubhepatic carinae	separate posteriorly, except a few specimens on 1 side	joining posteriorly in all specimens
1st abdominal segment carina	small anterior spine	no spine
Length 1st abdom. carina/lat. length 1st abdom. seg.	0.25—0.4	0.42—0.58
2nd abdominal segment carina	small posterior spine	no spine
dorsolateral spinules on telson	3 pairs	4—6 pairs
ovig. ♀, cl.	28—32.5 mm	42—50.5 mm

Table 5. Comparison of *Notostomus crosnieri* with Eastern Australian specimens.

Notostomus elegans A. Milne Edwards

Notostomus elegans A. Milne Edwards, 1881: 8; 1883, pl.31.—Crosnier & Forest, 1973: 56—63, figs 15, 16a,b.

Notostomus patentissimus Bate, 1888: 826—829, pl. 133, fig. 1, pl. 134, figs 1, 2.

Notostomus longirostris Bate, 1888: 833, pl. 135, fig. 4.

Material examined. New South Wales: AM P33144, east of Port Stephens, 32°59′S 153°03′E to 32°51′S 153°01′E, 495 m, midwater trawl, *Kapala* (K79-19-07), 29 Nov 1979; 1 specimen. AM P33145, east of Newcastle, 33°05′S 153°05′E to 33°13′S 153°05′E, 630 m, midwater trawl, *Kapala* (K79-19-03), 28 Nov 1979; 1 specimen. AM P35864, east of Newcastle, 33°07′S 153°11′E to 33°01′S 153°05′E, 630 m, midwater trawl, *Kapala* (K79-19-06), 28 Nov 1979; 1 specimen. AM P26604, north-east of Cape Howe, 37°24′S 150°30′E to 37°28′S 150°33′E, 0—540 m, midwater trawl, *Kapala* (K77-19-03), 1 Nov 1977; 2 specimens.

Diagnosis. Dorsal carina of carapace finely denticulate along its whole length; 5 lateral carinae on posterior carapace. All abdominal segments carinate, segments 3—6 with terminal medial spine. Upper lateral rostral carina not extending beyond orbital margin; lower lateral rostral carina not continuous with gastro-orbital carina; gastro-orbital carina not more strongly produced at posterior extremity. Tip of stylocerite reaching no further than midlength of second segment of antennular peduncle.

Remarks. These specimens agree with the description and figures of *N. elegans* given by Crosnier & Forest and the figures of the type of *N. westergreni* in the same paper (except for the denticle on the fifth pleuron). We have compared our

specimens with the types of *N. patentissimus* and *N. longirostris,* and in our opinion they are conspecific. They agree with the types in the following: 1) the upper lateral orbital carina which is horizontal, does not extend posteriorly behind the orbit; 2) the tip of the stylocerite reaches at least to the base and sometimes the midlength of the second segment of the antennular peduncle; 3) the spine on the scaphocerite (where still present) is subequal to, or less than the width across the scaphocerite at the base of the spine; 4) the dorsal carina slopes gradually to the posterior margin of the carapace; 5) the slope of the dorsal carina behind the orbit is similar; above the orbit the denticles of the carina are enlarged to only moderately sized teeth; 6) presence of a denticle at the posteroventral angle of the pleuron of the fifth abdominal segment; 7) the carina of the first abdominal segment is only moderately indented posteriorly; 8) the first and second abdominal segments have a submarginal carina on the pleuron; the first segment also has a carina in the form of an inverted 'Y' just below the articulation with the second segment; 9) presence of a carina curving posteriorly near the ventral margin on the anterior part of the pleura of abdominal segments 3—5; Crosnier & Forest (1973) noted that the spine at the tip of the scaphocerite is shorter in *N. elegans* than in *N. auriculatus.* To quantify this we have divided the length of the spine by the width across the scaphocerite at the base of the spine. In our specimens of *N. elegans* and the type of *N. longirostris* the spine is about four-fifths to subequal (0.8—0.90) to the width across the scaphocerite at the base of the spine. (The same ratio for *N. auriculatus* is 1.2—1.5.)

The anterior dorsal margin slopes slightly more steeply in *N. elegans* and in the types of *N. longirostris* and *N. patentissimus* than it does in *N. auriculatus.* We have measured the height of the dorsal carapace margin above the gastro-orbital carina both at the anterior extremity of the carina and at the point where the post-hepatic carina joins the gastro-orbital carina. In *N. elegans* the anterior height is about two-thirds (0.66—0.7) of the posterior height, while in *N. auriculatus* this ratio is about three-quarters (0.73—0.79).

On the other hand, the posterior dorsal margin, just anterior to the posterior carapace margin slopes more abruptly in *N. auriculatus* than in *N. elegans.*

The first abdominal segment is only moderately indented medially on the posterior margin while the length of the dorsal carina is about two-thirds to four-fifths the length of the segment at its articulation with the second segment.

The dactyls of pereopods 3 and 4 are less than one-fourth (0.2—0.23) the length of the propodi in *N. elegans* and the type of *N. longirostris;* the propodi and dactyls of pereopods 3—5 are detached in the type of *N. patentissimus.*

Crosnier & Forest (1973) stated that in *N. elegans* the submarginal carina usually extends anteriorly beyond the infra-subhepatic carina while in *N. auriculatus* it usually ends behind the infra-subhepatic carina. In the types of *N. longirostris* and *N. patentissimus* and one of our specimens (cl 24 mm) of *N. elegans* the submarginal carina extends anteriorly beyond the tip of the infra-subhepatic carina; in two other specimens (cl 17, 50.5 mm) the tips of the two carinae are at the same level, while in two other specimens (cl 42, 44.5 mm) the tip of the submarginal carina is behind that of the infra-subhepatic carina as it is in all our specimens of *N. auriculatus.*

The type of *N. westergreni* Faxon has been examined by one of us (BK); it was found that the infra-subhepatic carina extends anteriorly beyond the submarginal carina. Perhaps this character, as demonstrated above, is too variable to be of any use in separating species.

Our specimens were trawled at depths up to 630 m between 32°51′S and 37°28′S. *N. elegans* has not been recorded previously from eastern Australian waters.

Distribution. North and tropical Atlantic, eastern Australia, Celebes Sea *(N. patentissimus),* Banda Sea *(N. longirostris);* 630—2780 m.

Notostomus gibbosus A. Milne Edwards

Notostomus gibbosus A. Milne Edwards, 1881: 7; 1883, pl. 32.—Crosnier & Forest, 1973: 49—51, fig. 13.
Notostomus perlatus Bate, Kemp, 1913: 66—68, pl. 7, fig. 10; Chace, 1940: 170—171, fig. 42.

Material examined. New South Wales: AM P33150, 65 km east of Broken Bay, 33°31′S 152°20′E, 569 m, midwater trawl, *Kapala* (K77-24-02, JP77-18), 12 Dec 1977; 1 specimen.

Diagnosis. Dorsal carina of carapace finely denticulate along its whole length; four lateral carinae on posterior carapace. All abdominal segments carinate, segments 3—6 with terminal medial spine; no upper lateral rostral carina; lower lateral rostral carina continuous with gastro-orbital carina.

Remarks. This specimen agrees well with the figure of *N. gibbosus* given by Crosnier & Forest (1973) and with the specimen described and figured as *N. perlatus* by Kemp (1913). A full synonymy for this species is given by Crosnier & Forest (1973).

This species has not been recorded before from Australian waters nor from so far south; previous records have been from tropical waters.

Colour. The colour of the preserved specimen is uniformly pale red with darker red carinae.

Distribution. Indo-west Pacific, eastern and western Atlantic; 569—3932 m.

Oplophorus H. Milne Edwards, 1837

Oplophorus novaezeelandiae (de Man)

Hoplophorus novae-zeelandiae de Man, 1931: 369, figs. 1—20.

Oplophorus novaezeelandiae.—Yaldwyn, 1967: 3; Kensley, 1972: 38 (in key), fig. 17G,H; Crosnier & Forest, 1973: 26—27, fig. 5.

Material examined. New South Wales: AM P32795, 70 km east of Tuggerah Lake, 33°17′S 152°31′E to 33° 19′S 152°31′E, 0—90 m, midwater trawl, *Kapala* (K77-24-08), 13 Dec 1977; 2 specimens. AM P32791, 70 km east of Tuggerah Lake, 33°19′S 152°25′E to 33° 23′S 152°28′E, 0—630 m, midwater trawl, *Kapala* (K77-24-03), 13 Dec 1977; 1 specimen. AM P32794, 80 km east of Tuggerah Lake, 33°2O′S 152°34′E to 33° 24′S 152°31′E, 0—360 m, midwater trawl, *Kapala* (K77-24-09), 14 Dec 1977; 4 specimens. AM P32793, 90 km east of Tuggerah Lake, 33°25′S 152°32′E to 33°21′S 152°34′E, 0—360 m, midwater trawl, *Kapala* (K77-24-05), 13 Dec 1977; 1 specimen. AM P32796, off Port Hacking, 34°09′S 152°07′E to 34°20′S 152°02′E, approx. 550 m, midwater trawl, *Kapala* (JP71-2), 23 Mar 1971; 2 specimens. AM P32792, off Lake Illawarra, 34°40′S 151°15′E to 34°35′S 151°17′E, 594—675 m, fish trawl, *Kapala* (K77-19-05), 3 Nov 1977; 1 specimen. AM P32797, south of Montague Island, 36°24′S 150°18′E to 36°30′S 150°17′E, 126 m, fish trawl, *Kapala* (K77-19-01), 1 Nov 1977; 1 specimen. AM P32790, south-east of Twofold Bay, 37°24′S 150°30′E to 37°28′S 150°33′E, 540 m, fish trawl, *Kapala* (K77-19-03), 1 Nov 1977; 2 specimens.

Diagnosis. Rostrum at least twice carapace length, with spines on dorsal and ventral margins. Lateral margin of scaphocerite smooth. Posterolateral angle of carapace without spine. Third maxilliped and first pereopod with foliaceous exopods. Sixth abdominal segment not carinate, segments 3—5 with a dorsal carina terminating in long spine.

Remarks. The smooth outer margin of the scaphocerite distinguishes *O. novaezeelandiae* from other species of this genus.

These specimens were collected from 33°S to 37°30′S in trawls to a depth of 675 m.

This species has not previously been recorded off the eastern coast of Australia.

Distribution. South-west Indian Ocean, south-west Pacific and south-west Atlantic; 90—725 m.

Oplophorus spinosus (Brulle)

Palaemon spinosus Brulle, 1839: 18.

Oplophorus grimaldii.—Chace, 1940: 187—189, fig. 55; Kensley, 1972: 38 (in key), fig. 17I,J.

Oplophorus spinosus.—Holthuis, 1949: 229—230; 1955, fig. 1a; Crosnier & Forest, 1973: 25.

Material examined. Queensland: AM P32829, north-east of Danger Point, 28°02′S 153°59′E to 27°59′S 153°59′E, 540 m, prawn trawl, *Kapala* (K78-09-05), 2 June 1978; 1 specimen. AM P32803, north-east of Danger Point, 28°03′S 154°04′E to 28°01′S 154°04′E, 720 m, prawn trawl, *Kapala* (K78-23-08), 6 Nov 1978; 2 specimens. New South Wales: AM P17907, north-east of Coffs Harbour, 29°49′S 153°42′E to 29°59′S 153°38′E, 369 m, bottom trawl, *Kapala* (K71-09-04), 12 May 1971; 1 specimen. AM P32807, east of Newcastle, 32°51′S 153°01′E to 32°59′S 152°54′E, 630 m, midwater trawl, *Kapala* (K79-19-08), 29 Nov 1979; 1 specimen. AM P32834, east of Newcastle, 32°59′S 153°03′E to 32°51′S 153°01′E, 495 m, midwater trawl, *Kapala* (K79-19-07), 29 Nov 1979; 1 specimen. AM P32813, east of Newcastle, 33°03′S 152°58′E to 32°59′S 153°03′E, 630 m, midwater trawl, *Kapala* (K79-19-02), 27 Nov 1979; 6 specimens (2 ovig. ♀). AM P32806, south-east of Newcastle, 33°05′S 153°05′E to 33°13′S 153°05′E, 630 m, midwater trawl, *Kapala* (K79-19-03), 28 Nov 1979; 31 specimens (9 ovig. ♀). AM P32805, south-east of Newcastle, 33°07′S 153°11′E to 33°01′S 153°05′E, 630 m, midwater trawl, *Kapala* (K79-19-06), 28 Nov 1979; 1 specimen. AM P18100, south-east of Newcastle, 33°11′S 152°23′E, 576 m, Danish trawl, *Kapala* (K71-14-01), 10 Aug 1971; 4 specimens. AM P32823, east of Norah Head, 33°15′S 153°06′E to 33°20′S 153°04′E, 360 m, midwater trawl, *Kapala* (K79-19-04), 28 Nov 1979; 1 specimen. AM P32819, 70 km east of Tuggerah Lake, 33°17′S 152°31′E to 33°19′S 152°31′E, 0—90 m, midwater trawl, *Kapala* (K77-24-08), 13 Dec 1977; 17 specimens. AM P32804, east of Norah Head, 33°20′S 153°04′E to 33°12′S 153°13′E, 630 m, midwater trawl, *Kapala* (K79-19-05), 28 Nov 1979; 5 specimens (2 ovig. ♀). AM P32814, 80 km east of Tuggerah Lake, 33°20′S 152°32′E to 33°24′S 152°31′E, 0—360 m, midwater trawl, *Kapala* (K77-24-09), 14 Dec 1977; 208 specimens (79 ovig. ♀). AM P32822; 90 km east of Tuggerah Lake, 33°23′S 152°37′E to 33°19′S 152°39′E, 0—540 m, midwater trawl, *Kapala* (K77-24-06), 13 Dec 1977; 2 specimens. AM P32821, 90 km east of Tuggerah Lake, 33°25′S 152°32′E to 33°21′S 152°32′E, 0—360 m, midwater trawl, *Kapala* (K77-24-05), 13 Dec 1977; 3 specimens. AM P32812, 70 km east of Broken Bay, 33°19′S 152°25′E to 33°23′S 152°28′E, 0—630 m, midwater trawl, *Kapala* (K77-24-03), 13 Dec 1977; 129 specimens (67 ovig. ♀). AM P32830, 100 km east of Broken Bay, 33°28′S 152°34′E to 33°36′S 152°35′E, 0—630 m, midwater trawl, *Kapala* (K77-24-10), 14 Dec 1977; 88 specimens (30 ovig. ♀). AM P32817, 65 km east of Broken Bay, 33°31′S 152°20′E to 33°28′S 152°22′E, 0—540 m, midwater trawl, *Kapala* (K77-24-02), 12 Dec 1977; 270 specimens (111 ovig. ♀). AM P32808, east of Broken Bay, 33°32′S 152°06′E to 33°34′S 152°05′E, 810 m, prawn trawl, *Kapala* (K79-20-13), 6 Dec 1979; 2 specimens (1 ovig. ♀). AM P21068, east of Broken Bay, 33°32′S 152°00′E to 33°38′S 152°04′E, 810 m, prawn trawl, *Kapala* (K75-05-05), 19 Aug 1975; 1 specimen. AM P32809, east of Broken Bay, 33°34′S 152°04′E to 33°31′S 152°06′E, 720 m, prawn trawl, *Kapala* (K79-20-04), 4 Dec 1979; 1 specimen (ovig.). AM P30331, P32820, 70 km east of Broken Bay, 33°33′S 152°18′E to 33°35′S 152°17′E, 1—216 m, midwater trawl, *Kapala* (K77-24-01), 12 Dec 1977; 14 specimens (6 ovig. ♀). AM P19386, east of Long Reef, 33°41′S 151°53′E to 33°49′S 151°47′E, 450—441 m, Danish trawl, *Kapala* (K71-12-04), 20 July 1971; 1 specimen. AM P18976, east of Long Reef, 33°42′S 152°50′E to 33°48′S 152°54′E, 765 m, bottom trawl, *Kapala* (K72-07-15), 7 Dec 1972; 5 specimens. AM P18988, east of Long Reef, 33°43′S 151°55′E to 33°37′S 152°02′E, 675 m, bottom trawl, *Kapala* (K72-06-04), 19 Oct 1972; 2 specimens (1 ovig. ♀). AM P18980, east of Long Reef, 33°44′S 151°55′E to 33°40′S 151°58′E, 720 m, bottom trawl, *Kapala* (K72-07-

04), Nov 1971; 2 specimens (1 ovig. ♀). AM P18989, east of Sydney, 33°51′S 151°51′E to 33°45′S 151°55′E, 675 m, bottom trawl, *Kapala* (K72-06-03), 19 Oct 1972; 1 specimen. AM P32835, east of Sydney, 34°02′S 152°12′E to 34°14′S 152°14′E, about 600 m, midwater trawl, *Kapala* (JP71-8), 25—26 Mar 1971; 3 specimens. AM P32816, 65 km east of Sydney Heads, 34°05′S 152°02′E to 34°13′S 152°00′E, 0—630 m, midwater trawl, *Kapala* (K77-24-11), 14 Dec 1977; 2 specimens (1 ovig. ♀). AM P32826, east of Sydney, 34°05′S 151°56′E to 34°09′S 152°05′E, to 1200 m, midwater trawl, *Kapala* (JP71-1), 23 Mar 1971; 3 specimens. AM P32827, east of Sydney, 34°05′S 151°55′E to 34°10′S 152°14′E, about 950 m, midwater trawl, *Kapala* (JP71-6), 25 Mar 1971; 2 specimens. AM P32800, south-east of Sydney, 34°10′S 152°16′E to 34°00′S 152°14′E, about 350 m, midwater trawl, *Kapala* (JP71-7), 25 Mar 1971; 18 specimens. AM P32799, south-east of Sydney, 34°10′S 151°59′E to 34°09′S 152°05′E, about 60 m, midwater trawl, *Kapala* (JP71-3), 24 Mar 1971; 22 specimens. AM P32828, south-east of Sydney, 34°09′S 152°07′E to 34°14′S 152°14′E, about 250 m, midwater trawl, *Kapala* (JP71-4), 24—25 Mar 1971; 1 specimen. AM P32798, south-east of Sydney, 34°09′S 152°07′E to 34°20′S 152°02′E, about 550 m, midwater trawl, *Kapala* (JP71-2), 23 Mar 1971; 67 specimens. AM P32801, 80 km east of Lake Illawarra, 34°20′S 151°56′E to 34°25′S 151°54′E, 0—630 m, midwater trawl, *Kapala* (K77-24-12), 14 Dec 1977; 12 specimens (2 ovig. ♀). AM P32810, east of Kiama, 34°40′S 151°15′E to 34°35′S 151°17′E, 594—675 m, midwater trawl, *Kapala* (K77-19-05), 3 Nov 1977; 46 specimens (24 ovig. ♀). AM P32815, east of Nowra, 34°55′S 151°13′E to 34°53′S 151°14′E, 810 m, demersal trawl, *Kapala* (K78-27-05), 12 Dec 1978; 2 specimens (1 ovig. ♀). AM P32811, east of Brush Island, 35°36′S 150°55′E to 35°39′S 150°59′E, 540 m, midwater trawl, *Kapala* (K77-18-05), 27 Oct 1977; 4 specimens (2 ovig. ♀). AM P21818, south of Montague Island, 36°24′S 150°18′E to 36°30′S 150°17′E, 126 m, bottom trawl, *Kapala* (K77-19-01), 1 Nov 1977; 6 specimens. AM 32802, south-east of Twofold Bay, 37°24′S 150°30′E to 37°28′S 150°33′E, 540 m, midwater trawl, *Kapala* (K77-19-03), 1 Nov 1977; 13 specimens (1 ovig. ♀).

Diagnosis. Rostrum less than twice carapace length, with spines on dorsal and ventral margins. Lateral margin of scaphocerite spinose, inner margin with a distal barb. Anterolateral angle of carapace without a hooked spine. Third maxilliped and first pereopod with foliaceous exopods. Sixth abdominal segment not carinate, segments 3—5 with a dorsal carina terminating in long spine.

Remarks. In some of our specimens there is a tubercle at the posterolateral angle of the carapace but this is not curved forwards like the hooked spine in *O. gracilirostris*. In addition, the lateral carina above the orbit converges posteriorly towards the midline in *O. spinosus*, while in *O. gracilirostris* it is subparallel to the midline. *O.spinosus* is distinguished from *O. novaezeelandiae* by the scaphocerite which has a spinose, rather than a smooth, outer margin, and from *O. spinicauda* by the lack of a terminal spine dorsally on the second abdominal segment.

These specimens were collected between 28°S and 37°30′S in trawls down to 1200 m.

Distribution. West and east Atlantic, Indo-west Pacific; 75—1200 m.

Systellaspis Bate, 1888

Systellaspis debilis (A. Milne Edwards)

Acanthephyra debilis A. Milne Edwards, 1881: 13.
Systellaspis debilis.—Chace 1940: 181—184, figs 51—53; Kensley, 1972: 38, fig. 17B, C; Crosnier & Forest, 1973: 87—92, figs 26b, 27b.

Material examined. New Caledonia: AM P32983, 19°55′S 170°00′E, 0—550 m, midwater trawl, *Kimbla* (K4/71-8), 12 May 1971; 4 specimens. AM P32984, 19°52′S 170°00′E, 0—275 m, midwater trawl, *Kimbla* (K4/71-7), 12 May 1971; 20 specimens. AM P32985, 21°05′S 166°45′E, 0—925 m, midwater trawl, *Kimbla* (K4/71-5), 9 May 1971; 11 specimens (1 ovig. ♀).

New South Wales: AM P32998, 80—128 km east of Newcastle, 33°03′S 152°58′E to 32°59′S 153°03′E, 630 m, midwater trawl, *Kapala* (K79-15-02), 27 Nov 1979; 12 specimens. AM P32997, 80—128 km east of Newcastle, 33°05′S 153°05′E to 33°13′S 153°05′E, 630 m, midwater trawl, *Kapala* (K79-19-03), 28 Nov 1979; 34 specimens (16 ovig. ♀). AM P32991, 70 km east of Tuggerah Lake, 33°17′S 152°31′E to 33°19′S 152°31′E, 0—90 m, midwater trawl, *Kapala* (K77-24-08), 13 Dec 1977; 12 specimens (1 ovig. ♀). AM P32994, 70 km east of Broken Bay, 33°19′S 152°25′E to 33°23′S 152°28′E, 0—630 m, midwater trawl, *Kapala* (K77-24-03), 13 Dec 1977; 13 specimens (3 ovig, ♀). AM P32993, 80—128 km east of Tuggerah Lake, 33°20′S 153°04′E to 33°12′S 153°13′E, 630 m, midwater trawl, *Kapala* (K79-19-05), 28 Nov 1979; 34 specimens (11 ovig. ♀). AM P32992, 80 km east of Tuggerah Lake, 33°20′S 152°32′E to 33°24′S 152°31′E, 0—360 m, midwater trawl, *Kapala* (K77-24-09), 14 Dec 1977; 19 specimens (6 ovig. ♀). AM P30990, 90 km east of Tuggerah Lake, 33°23′S 152°37′E to 33°19′S 152°39′E, 0—540 m, midwater trawl, *Kapala* (K77-24-06), 13 Dec 1977; 2 specimens. AM P32996, 100 km east of Broken Bay, 33°28′S 152°34′E to 33°36′S 152°35′E, 0—630 m, midwater trawl, *Kapala* (K77-24-10), 14 Dec 1977; 21 specimens (7 ovig. ♀). AM P25061, east of Broken Bay, 33°30′S 152°05′E to 33°27′S 152°07′E, 806—810 m, trawl, *Kapala* (K76-24-04), 21 Dec 1976; 1 specimen. AM P32988, 65 km east of Broken Bay, 33°31′S 152°20′E to 33°28′S 152°22′E, 0—540 m, midwater trawl, *Kapala* (K77-24-02), 12 Dec 1977; 14 specimens (5 ovig. ♀). AM P30330, 70 km east of Broken Bay, 33°33′S 152°18′E to 33°35′S 152°17′E, 216 m, midwater trawl, *Kapala* (K77-24-01), 12 Dec 1977; 16 specimens (4 ovig. ♀). AM P25124, east of Broken Bay, 33°35′S 152°01′E to 33°32′S 152°03′E, 810 m, midwater trawl, *Kapala* (K76-24-03), 20 Dec 1976; 1 ovig. ♀. AM P32987, east of Broken Bay, 33°35′S 152°00′E to 33°33′S 152°02′E, 810 m, demersal trawl, *Kapala* (K77-23-12), 8 Dec 1977; 1 specimen. AM P32982, south-east of Sydney, 34°02′S 152°12′E to 34°14′S 152°14′E, 0—600 m, midwater trawl, *Kapala* (JP71-8), 25—26 Mar 1971; 5 specimens. AM P32980, south-east of Sydney, 34°05′S 151°56′E, 0—1200 m, midwater trawl, *Kapala* (JP71-1), 23 Mar 1971; 126 specimens (5 ovig. ♀). AM P32981, south-east of Sydney, 34°05′S 151°22′E to 34°10′S 152°14′E, 0—950 m, midwater trawl, *Kapala* (JP71-6), 25 Mar 1971; 21 specimens. AM P32979, south-east of Sydney, 34°10′S 152°16′E to 34°00′S 152°14′E, about 350 m, midwater

trawl, *Kapala* (JP71-7), 25 Mar 1971; 1 specimen. AM P32977, south-east of Sydney, 34°10′S 151°59′E to 34°09′S 152°05′E, 0—60 m, midwater trawl, *Kapala* (JP71-3), 24 Mar 1971; 155 specimens (2 ovig. ♀). AM P32978, south-east of Sydney, 34°09′S 152°07′E to 34°14′S 152°14′E, 0—about 250 m, midwater trawl, *Kapala* (JP71-4), 24—25 Mar 1971; 2 specimens. AM P32976, south-east of Sydney, 34°09′S 152°07′E to 34°20′S 152°02′E, 0—about 550 m, midwater trawl, *Kapala,* (JP71-2), 23 Mar 1971; 1 specimen. AM P32999, 80 km east of Lake Illawarra, 34°20′S 151°56′E to 34°25′S 151°54′E, 0—630 m, midwater trawl, *Kapala* (K77-24-12), 14 Dec 1977; 6 specimens (2 ovig. ♀). AM P33001, off Port Kembla, 34°28′S 151°29′E, 0—225 m, midwater trawl, *Kapala* (K74-05-JP1), 22 Jan 1974; 5 specimens. AM P32986, east of Kiama, 34°40′S 151°15′E to 34°35′S 151°17′E, 594—675 m, midwater trawl, *Kapala* (K77-19-05), 3 Nov 1977; 2 specimens. AM P32989, east of Brush Island, 35°36′S 150°55′E to 35°39′S 150°59′E, 540 m, lightfish net trawl, *Kapala* (K77-18-05), 27 Oct 1977; 8 specimens (1 ovig. ♀). AM P33000, off Cape Howe, 37°24′S 150°30′E to 37°28′S 150°33′E, 0—540 m, midwater trawl, *Kapala* (K77-19-03), 1 Nov 1977; 8 specimens (2 ovig. ♀).

Diagnosis. Rostrum slender, usually longer than carapace length, with evenly spaced spines on dorsal and ventral margins. No dorsal or lateral carina running the entire length of the carapace; only third and part of fourth abdominal segments carinate; third segment with a large terminal dorsal spine; posterior margin of fourth and fifth segments denticulate on either side of a small median spine.

Remarks. *S. debilis* is the only species of *Systellapsis* represented in this collection. This species is distinguished by the presence of denticulations on the posterior margin of the fourth and fifth abdominal segments.

These specimens were collected off New Caledonia between 19°50′S and 21°S in trawls at depths to 1200 m.

Distribution. Western and eastern Atlantic, Indo-west Pacific; 150—1500 m.

Family NEMATOCARCINIDAE

Nematocarcinus A. Milne Edwards, 1881

Nematocarcinus gracilis Bate

Nematocarcinus gracilis Bate, 1888: 815, pl. 132, fig. 8.—Chace, 1986: 71, fig. 38.

Material examined. New South Wales: AM P25059, east of Broken Bay, 33°30—27′S 152°05—07′E, 808 m, demersal prawn trawl, *Kapala* (K76-24-04), 21 Dec 1976; 1 ♂. AM P25099, east of Broken Bay, 33°30?-27′S 152°05—07′E, 808 m, demersal prawn trawl, *Kapala* (K76-24-04), 21 Dec 1976; 1 ♀. AM P25128, east of Broken Bay, 33°30—27′S 152°05—07′E, 808 m, demersal prawn trawl, *Kapala* (K76-24-04), 21 Dec 1976; 2 ♂, 1 ♀.

Diagnosis. Rostrum nearly horizontal, not reaching end of antennular peduncle, with 13—22 evenly spaced, basally articulated, dorsal spines and single distal fixed ventral spine. Pleuron of abdominal segment 5 with acute posteroventral tooth. Abdominal segment 6 lacking ventral tubercles. Pereopods 3 and 4 with dactyl shorter than propod.

Distribution. Arabian Sea to Hawaii; Philippines; 165—1170 m.

Nematocarcinus undulatipes Bate

Nematocarcinus undulatipes Bate, 1888: 801, pl. 130.—Chace, 1986: 76, figs 41, 42.

Material examined. New South Wales: AM P25096, east of Broken Bay, 33°30—27′S 152°05—07′E, 808 m, *Kapala* (K76-24-04), 21 Dec 1976; 1 ♂, 1 ♀. AM P25097, east of Broken Bay, 33°30—27′S 152°05—07′E, 808 m, *Kapala* (K76-24-04), 21 Dec 1976; 1 ♂. AM P25141, east of Broken Bay, 33°35′S 152°01′E, 810 m, *Kapala* (K76-24-03), 20 Dec 1976; 3 ♂, 2 ovig. ♀. AM P26762, south-east of Newcastle, 33°11—09′S 152°24′E, 732 m, *Kapala* (K77-23-10), 7 Dec 1977; 6 ♂, 26 ovig. ♀, 1 ♀. AM P26764, south-east of Newcastle, 33°11—09′S 152°24′E, 732 m, *Kapala* (K77-23-10), 7 Dec 1977; 13 ovig. ♀, 6 ♀. AM P26791, east of Broken Bay, 33°35′S 152°00′E, 823 m, *Kapala* (K77-23-12), 8 Dec 1977; 4 ovig. ♀, 1 ♀.

Diagnosis. Rostrum nearly horizontal, with 7—14 dorsal articulated teeth, posterior teeth closely spaced, becoming more widely spaced anteriorly; single distal ventral fixed tooth. Rostrum not, or barely reaching end of antennular peduncle. Pleuron of fifth abdominal segment with acute posteroventral tooth. Sixth abdominal segment lacking ventral tubercles.

Distribution. Western Indian Ocean, Philippines, Indonesia, to Kermadec Islands; 366—1269 m.

Family STYLODACTYLIDAE

Parastylodactylus Figueira, 1971

Parastylodactylus sp.

Fig. 6

Material examined. New South Wales: AM P35911, north-east of Danger Point, 27°55′S 154°03′E to 27°51′S 154°03′E, 540 m, prawn trawl, *Kapala* (K78-23-09), 6 Nov 1978; 1 ovig. ♀, cl. 9.1 mm.

Remarks. The present specimen shows several differences from *P. bimaxillaris* (Bate, 1888) (see Chace, 1983: 8, fig. 4), the only species in the genus. These differences include the presence of a stronger posteroventral spine on abdominal somite 6; a stronger posteroventral spine on pleuron 5; three clumps of setae on the distal eyestalk (a single row in *P. bimaxillaris);* a larger carapace (length 9.1 mm as against 6.7—7.1 mm) in the ovigerous female; a higher rostral tooth count (40+/9+) against 20—22/5—9 in *P. bimaxillaris;* the merus of pereopod 2 bears eight to nine spines (unarmed in *P. bimaxillaris);* the posterior three pairs of pereopods are unarmed

except for a single distal spine *(P. bimaxillaris* has two to three additional meral spines); and a basally more elongate stylocerite of the antennule than in *P. bimaxillaris.* These differences would indicate that this specimen belongs to an undescribed species of *Parastylodactylus.* Unfortunately, as the specimen has a damaged rostrum and tailfan, and lacks several of the pereopods, it was decided not to designate a new species.

Stylodactylus A. Milne Edwards, 1881

Stylodactylus libratus Chace

Stylodactylus libratus Chace, 1983: 12, fig. 5.

Material examined. New South Wales: AM P35909, north-east of Danger Point, 27°55'S 154°03'E to 27°57'S 154°03'E, 540 m, prawn trawl, *Kapala* (K78-23-09), 6 Nov 1979; 1 ♀, cl. 13.0 mm.

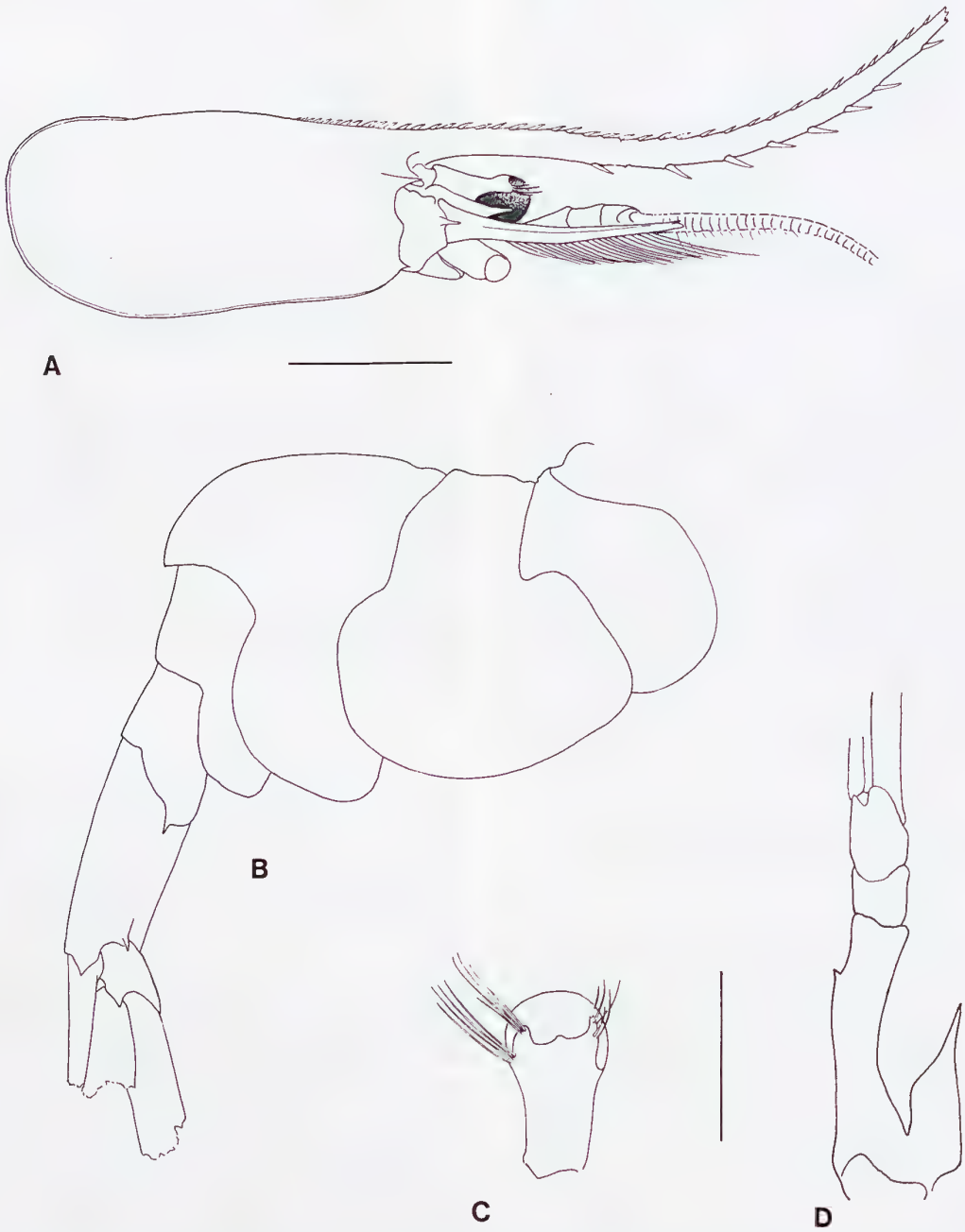

Fig. 6. *Parastylodactylus* sp. **A,** carapace in lateral view; **B,** abdomen in lateral view; **C,** eye; **D,** antenna 1; (Scales: A,B = 5 mm, C,D = 3 mm).

Diagnosis. Supraorbital spine large. Single spine below prominent branchiostegal spine. Rostrum almost horizontal, tooth format 22/5. All abdominal pleura rounded. Telson twice longer than wide, with 3 or 4 pairs of dorsal spines and strong mid-dorsal point on posterior margin flanked by 2 pairs of spines. Scaphocerite with 4—5 elongate spines on outer margin.

Remarks. The description of *Stylodactylus libratus* was based on a single male specimen, thus the degree of variation of morphological characters is unknown. While the present specimen agrees in most points with the description of *S. libratus,* a few differences are apparent: article 2 of the antennular peduncle is not subequal in length to article 3, but twice its length; there are fewer rostral teeth (22/5 as against 31/8); there is only one, not two secondary branchiostegal spines on the carapace; the pereopods exhibit a heavier dorsal and lateral spination than in *S. libratus.* As these differences, however, could be within the range of variation of the species, it is thought best not to describe the single specimen as a new species.

Stylodactylus multidentatus Kubo

Stylodactylus multidentatus Kubo, 1942: 34, figs 4,5.—Chace, 1983: 20, fig. 8.

Material examined. New South Wales: AM P21029, north-east of Wollongong, 34°16—22′S 151°26—23′E, 356 m, demersal prawn trawl, *Kapala* (K75-05-01), 8 Aug 1975; 1 male. AM P24475, east of Sydney, 33°39—36′S 151°54—57′E, 356 m, *Kapala* (K76-07-06), 27 May 1976; 1 female. AM P24484, east of Sydney, 33°35—30′S 151°59′—152°02′E, 356 m, *Kapala* (K76-09-02), 24 June 1976; 1 male.

Diagnosis. Carapace with 2 spines on anteroventral margin; strong supraorbital spine present. Rostrum armed with 14—23 ventral spines. Antennal scale with spines on lateral margin. Abdominal pleura rounded. Posterior telsonic margin lacking median spine.

Distribution. Southern Japan; Philippines; 152—366 m.

Family PASIPHAEIDAE

Eupasiphae Wood-Mason & Alcock, 1893

Eupasiphae gilesii (Wood-Mason & Alcock)

Parapasiphaë (Eupasiphaë) Gilesii Wood-Mason & Alcock, 1893: 166.
Eupasiphae gilesii.—Crosnier & Forest, 1973: 150, fig. 44; Kensley, 1977: 32, fig. 10B.

Material examined. New South Wales: AM P26568, north-east of Batemans Bay, 35°36′S 150°55′E to 35°39′S 150°56′E, 540 m, midwater trawl, *Kapala* (K77-18-05), 27 Oct 1977; 1 ♀. AM P26835, north-east of Broken Bay, 33°31′S 152°20′E to 33°28′S 152°32′E, 630 m, midwater trawl, *Kapala* (K77-24-03), 13 Dec 1977; 1 ovig. ♀, 1 juv. AM P33066, north-east to east of Broken Bay, 33°28′S 152°34′E to 33°36′S 152°35′E, 630 m, midwater trawl, *Kapala* (K77-24-10), 14 Dec 1977; 1 juv. AM P33067, north-east to east of Wollongong, 34°20′S 151°56′E to 34°25′S 151°54′E, 630 m, midwater trawl, *Kapala* (K77-24-12), 14 Dec 1977; 2 juvs. AM P33063, south-east of Newcastle, 33°03′S 152°58′E to 32°59′S 153°03′E, 482 m, midwater trawl, *Kapala* (K79-19-02), 27 Nov 1979; 1 ovig. ♀. AM P33062, north-east of Norah Head, 33°05′S 153°05′E to 33°13′S 153°05′E, 630 m, midwater trawl, *Kapala* (K79-19-03), 28 Nov 1979; 1 juv. AM P33064, south-east of Newcastle, 33°07′S 153°11′E to 33°01′S 153°05′E, 630 m, midwater trawl, *Kapala* (K79-19-06), 28 Nov 1979; 2 ♂. AM P33065, east of Newcastle, 32°59′S 153°03′E to 32°51′S 153°01′E, 391 m, midwater trawl, *Kapala* (K79-19-07), 29 Nov 1979; 1 ♂. AM P33068, south-east of Port Jackson to north-east of Wollongong, 34°02′S 152°12′E to 34°14′S 152°14′E, 0—600 m, midwater trawl, *Kapala* (JP71-8), 25 Mar 1971; 1 juv.

Diagnosis. Dorsal postrostral and carapace carina serrate throughout. Antennal and branchiostegal spines present. Mandibular palp of 2 articles. Maxilliped 3 with 2 arthrobranchs. Pereopod 4 shorter than either pereopods 3 or 5.

Remarks. This would seem to be the first Pacific record of a species widespread throughout the Atlantic and Indian oceans.

Distribution. Bermuda; Cape Verde Islands; Canary Islands; Madeira; off Natal, South Africa; Arabian Sea; Gulf of Oman; Andaman Sea; 340-770 m.

Parapasiphae Smith, 1884

Parapasiphae sulcatifrons Smith

Parapasiphaë sulcatifrons Smith, 1884: 384, pl.5, fig.4, pl.6, figs 1—7.
Parapsiphae sulcatifrons.—Crosnier & Forest, 1973: 142, fig. 41.

Material examined. New South Wales: AM P26566, north-east of Batemans Bay, 35°36′S 150°55′E to 35°39′S 150°56′E, 540 m, midwater trawl, *Kapala* (K77-18-05), 27 Oct 1977; 1 ♀, 1 juv. AM P26567, north-east of Batemans Bay, 35°36′S 150°55′E to 35°39′S 150°56′E, 540 m, midwater trawl, *Kapala* (K77-18-05), 27 Oct 1977; 4 ♂, 4 ♀, 2 juvs. AM P33076, north-east of Cape Howe, 37°24′S 150°30′E to 37°28′S 150°33′E, 540 m, midwater trawl, *Kapala* (K77-19-03), 1 Nov 1977; 18 specimens. AM P33073, north-east of Broken Bay, 33°31′S 152°20′E to 33°28′S 152°22′E, 569 m, midwater trawl, *Kapala* (K77-24-02), 12 Dec 1977; 3 ♂, 3 ovig. ♀, 4 ♀. AM P33075, north-east of Broken Bay, 33°27′S 152°30′E to 33°23′S 152°32′E, 630 m, midwater trawl, *Kapala* (K77-24-03), 13 Dec 1977; 14 specimens. AM P33074, north-east to east of Broken Bay, 33°28′S 152°34′E to 33°36′S 152°35′E, 630 m, midwater trawl, *Kapala* (K77-24-10), 14 Dec 1977; 27 juvs. AM P33077, north-east to east of Wollongong, 34°20′S 151°56′E to 34°25′S 151°54′E, 630 m, midwater trawl, *Kapala* (K77-24-12), 14 Dec 1977; 1 juv.

Diagnosis. Mandibular palp of 2 articles. Carapace lacking antennal and branchiostegal spines;

mid-dorsal carapace carina unarmed, anteriorly sulcate. Fingers of chela of pereopod 2 not longer than palm. Pereopod 4 shorter than either pereopods 3 or 5.

Remarks. This would seem to be the first record of the species from the western Pacific.

Distribution. North and south Atlantic; Indian Ocean; off west coast of U. S. A.; 500—5340 m.

Pasiphaea Savigny, 1816

Pasiphaea berentsae n. sp.

Figs 7—9

Type material. New South Wales: HOLOTYPE: AM P26768, north-east of Norah Head, 33°11′S 152°24′E to 33°09′S 152°25′E, 720 m, demersal prawn trawl, *Kapala* (K77-23-10), 7 Dec 1977; 1 ovig. ♀, cl 47.2 mm. PARATYPES: AM P26797, north-east of Broken Bay, 33°27′S 152°09′E to 33°25′S 152°11′E, 874 m, demersal prawn trawl, *Kapala* (K77-23-13), 8 Dec 1977; 1 ♀, cl 43.1 mm. AM P26798, north-east of Broken Bay, 33°27′S 152°09′E to 33°25′S 152°11′E, 874 m, demersal prawn trawl, *Kapala* (K77-23-13), 8 Dec 1977; 2 ♂, cl 29.0, 30.8 mm, 13 ♀, cl 33.0—44.1 mm. AM P26779, south-east of Broken Bay, 33°40—35′S 151°56—58′E, 714—732 m, demersal prawn trawl *Kapala* (K77-23-05), 6 Dec 1977; 5 ♀, cl 30.0—37.4 mm. USNM 211394, north-east of Broken Bay, 33°27′S 152°09′E to 33°25′S 152°11′E, 874 m, demersal prawn trawl, *Kapala* (K77-23-13), 8 Dec 1977; 1 ovig. ♀, cl 37.8 mm, 1 ♀, cl 43.2 mm.

Diagnosis. Carapace dorsally carinate. Abdominal somites 2—6 dorsally carinate. Posterior margin of telson deeply notched. Pereopod 1, merus

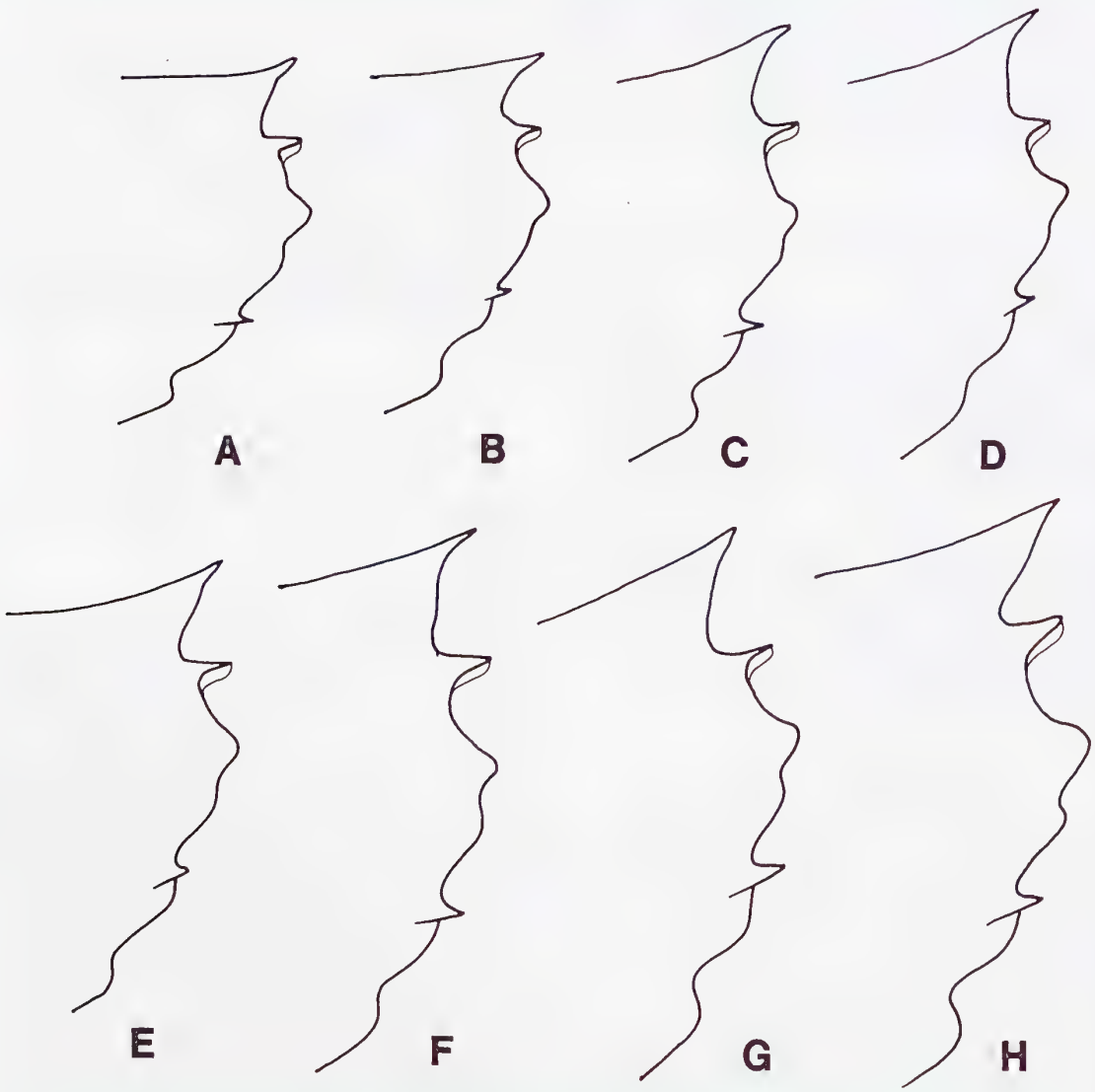

Fig. 7. *Pasiphae berentsae* n. sp., anterior carapace variation. **A,** ♂ cl 30.8 mm; **B,** ♂ cl 29.0 mm; **C,** ♀ cl 33.0 mm; **D,** ♀ cl 40.5 mm; **E,** ovig. ♀ cl 37.8 mm; **F,** ♀ cl 33.0 mm; **G,** ♀ cl 42.5 mm; **H,** ♀ cl 44.1 mm.

armed with 0—3 spines; pereopod 2, merus armed with 12—17 spines, ischium with 0—1 spine, basis with 1—5 spines.

Description. Rostrum just reaching anterior carapace margin, directed obliquely upward, anteriorly narrowed into spine-like extremity, anterior margin oblique, slightly convex, straight, or slightly concave. Carapace dorsally carinate almost to posterior margin; with strong suprabranchial ridge extending almost to posterior margin; branchiostegal spine marginal, strong, non-carinate. Abdominal somite 1 dorsally rounded; somites 2—6 dorsally carinate, all somites lacking posterodorsal spine. Pleuron 1 ventrally straight; pleuron 2 broadly rounded, pleura 3 and 4 ventrally straight, with rounded lobe-like extension anteriorly; pleuron 5 subrectangular, ventral margin faintly concave. Somite 6 1.5X length of somite 5, subequal to telson in length. Telson dorsally grooved, posterior margin deeply cleft, bearing 7 pairs of spines.

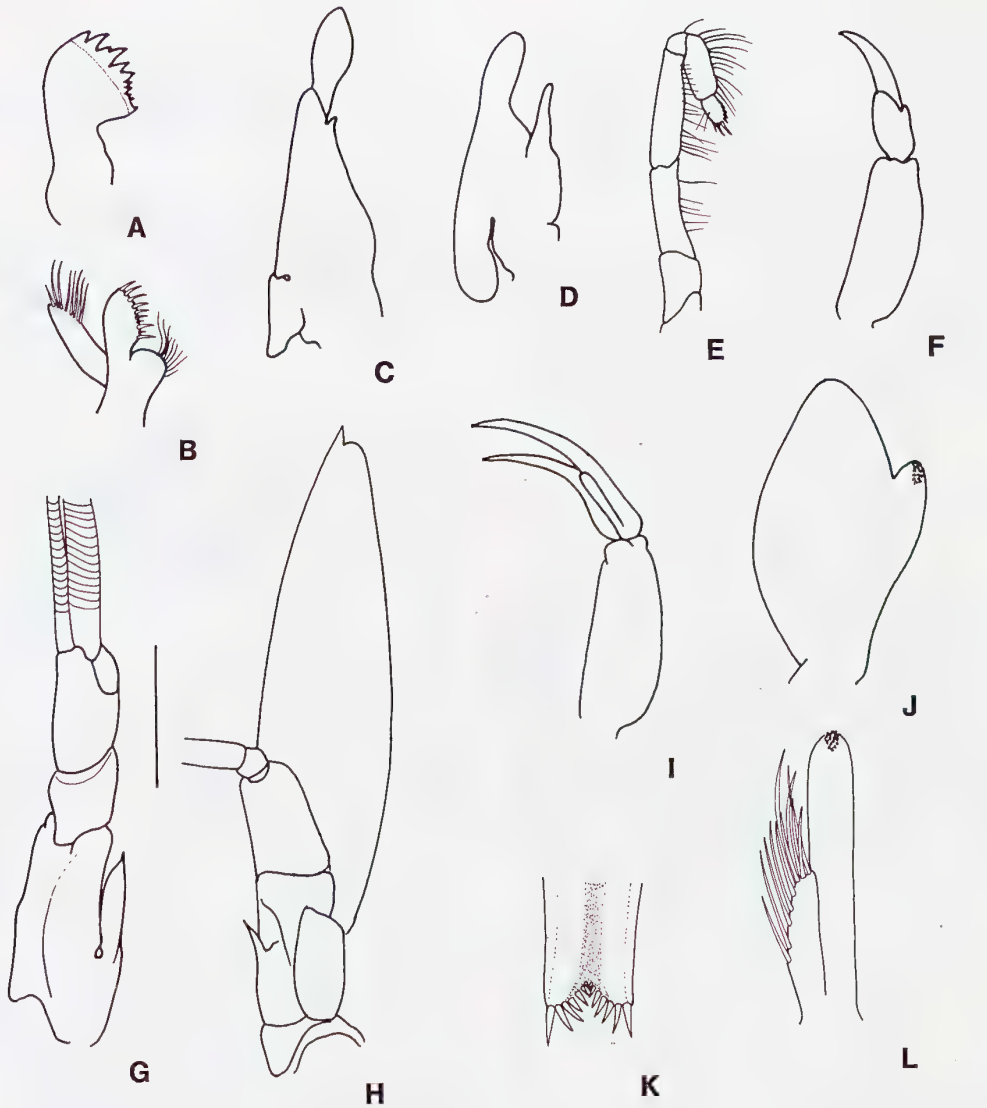

Fig. 8. *Pasiphae berentsae* n. sp. **A**, mandible; **B**, maxilla 1; **C**, maxilliped 1; **D**, maxilla 2; **E**, maxilliped 3; **F**, pleopod 1 ♂; **G**, antenna 1; **H**, antenna 2; **I**, pleopod 2 ♂; **J**, pleopod 1 ♂, endopod; **K**, apex of telson; **L**, pleopod 2 ♂, appendix masculina and appendix interna enlarged. (Scales: G=4 mm)

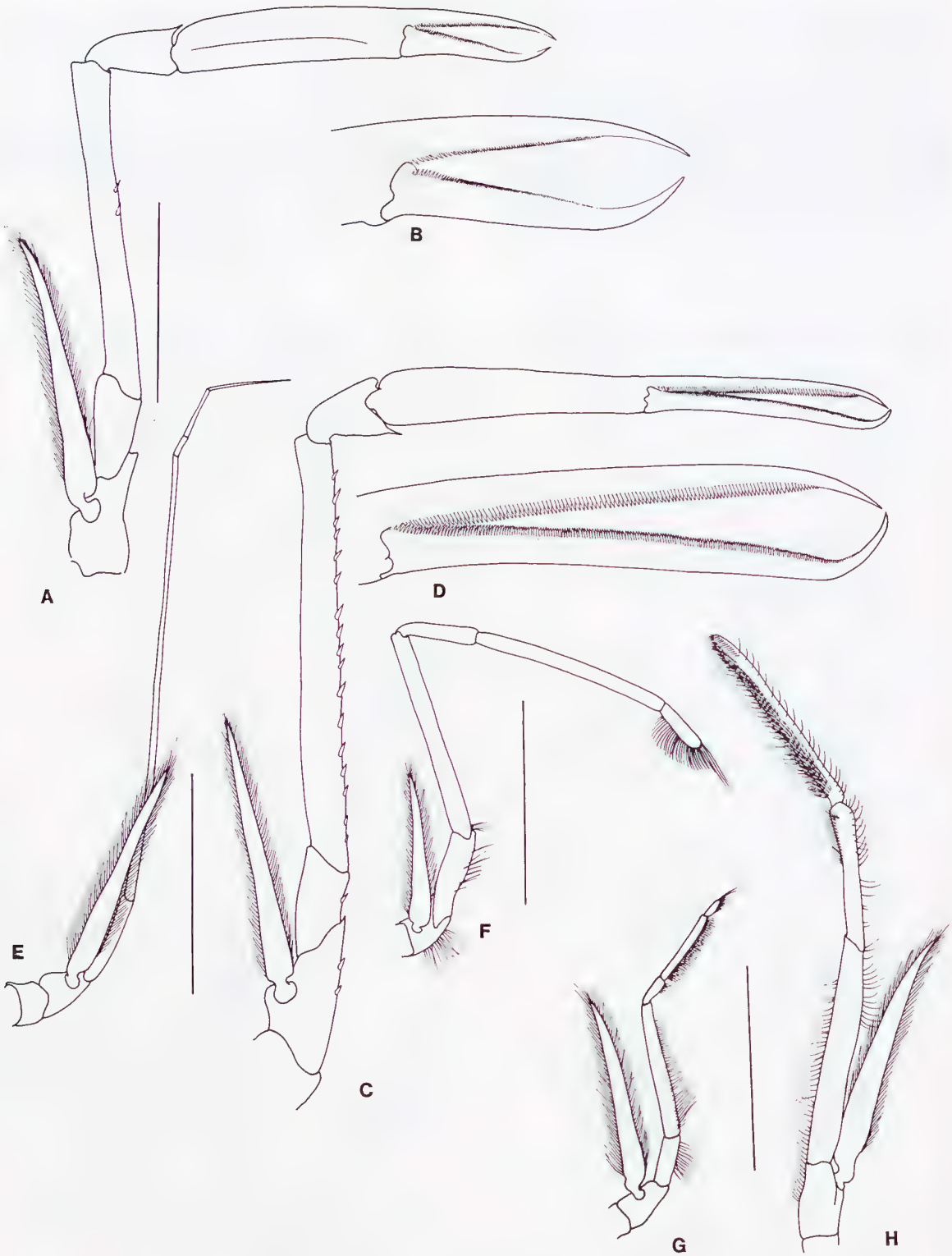

Fig. 9. *Pasiphae berentsae* n.sp. **A,** pereopod 1; **B,** pereopod 1, chela enlarged; **C,** pereopod 2; **D,** pereopod 2, chela enlarged; **E,** pereopod 3; **F,** pereopod 5; **G,** pereopod 4; **H,** maxilliped 3. (Scales: A,C,E-H = 10 mm).

Antenna 1, stylocerite twisted, distally acute, almost reaching distal margin of basal peduncular segment; segment 2 less than half length of basal segment, ventromesial margin with slight shoulder at about midlength. Antenna 2 overreaching peduncle of antenna 1 by slightly more than half of blade-length; scaphocerite with outer margin gently convex; distal spine extending well beyond apex of blade; strong elongate ventrodistal spine on peduncle segment 2.

Mouthparts as illustrated. Maxilliped 3 not quite reaching distal spine of scaphocerite; distal segment apically subacute, about 1.4X length of segment 2, with dense bands of spines on ventral margin, and subterminal clump of ventrally directed spines; segment 2 with dense patch of ventrodistal setae.

Pereopod 1 over-reaching scaphocerite by half length of fingers of chela; fingers about 0.6X length of palm; palm about 2.6X length of carpus; merus 4X length of carpus, with 0—3 spines on posterior margin.

Pereopod 2 over-reaching scaphocerite by length of fingers of chela; palm about 1.2X length of fingers; carpus slightly less than ¼ length of palm, with strong ventrodistal spine; merus 7X length of carpus, with 12—17 spines on posterior margin; ischium with 0—1 posterior spine; basis with 1—5 posterior spines.

Pereopod 3 very slender, reaching to distal margin of merus of pereopod 1.

Pereopod 4 shorter than either pereopod 3 or 5, reaching to distal margin of carpus of pereopod 5; dactylus ovate, setose; propodus with dense band of setae on ventral margin. Pereopod 5 reaching to midlength of merus of pereopod 2; dactylus distally rounded, with fringe of setae on posteroventral margins; propodus almost 4X length of dactylus, 2.5X length of carpus.

Pleopod 1 of male, endopod roughly ovate, with rounded lobe bearing tiny hooks on mesial margin. Pleopod 2 of male with appendix masculina half length of appendix interna, bearing 12 elongate spines on mesial and distal margins.

Inner uropodal ramus exceeding telson by ¼ of its length; outer ramus exceeding inner by ¼ of its length.

Remarks. *Pasiphaea berentsae* differs from *P. meiringnaudei* Kensley, 1977, which it closely resembles, in having fewer spines on the segments of pereopod 2, in having a shorter stylocerite, a shallower telsonic notch, more spines on the appendix masculina, and in the female becoming ovigerous at a smaller size (cl 50 to 58 mm in the South African species).

While many of the diagnostic characters of this species agree with those of *P. tarda* Kroyer, the shape of the rostrum and the telsonic notch differ markedly.

The species is most easily separated from *P. barnardi* Yaldwyn, 1971, by the possession of spination on the bases of pereopod 2.

Etymology. The species is named for Penelope B. Berents of the Australian Museum, in thanks for her assistance with the sorting and cataloguing of the *Kapala* collection.

Distribution. Off New South Wales, 720—874 m.

Pasiphaea kapala n. sp.

Figs 10—12

Type material. New South Wales: HOLOTYPE: AM P33133, north-east of Norah Head, 33°08′S 152°27′E to 33°10′S 152°24′E, 580 m, demersal prawn trawl, *Kapala* (K77-23-09), 7 Dec 1977; 1 ♂, cl 24.5 mm. PARATYPES: AM P26789, east of Broken Bay, 33°35—33′S 152°00—02′E, 823 m, demersal prawn trawl, *Kapala* (K77-23-12), 8 Dec 1977; 27 ♂, cl 22.5—28.2 mm, 23 ♀, cl 22.6—26.0 mm. USNM 211393, north-east of Yamba, 29°26′S 153°49′E to 29°20′S 153°50′E, 450 m, demersal prawn trawl, *Kapala* (K75-09-08), 12 Oct 1975; 20 ♂, cl 22.0—25.6 mm, 20 ♀, cl 22.0—25.8 mm.

Additional material examined. New South Wales: AM P20999, east of Broken Bay, 33°32′S 152°04′E to 33°38′S 152°00′E, 810 m, demersal prawn trawl, *Kapala* (K75-05-05), 19 Aug 1975; 1 ♀. AM P21070, east of Broken Bay, 33°32′S 152°04′E to 33°38′S 152°00′E, 810 m, demersal prawn trawl, *Kapala* (K75-05-05), 19 Aug 1975; 1 ♂. AM P21075, east of Broken Bay, 33°32′S 152°04′E to 33°38′S 152°00′E, 810 m, demersal prawn trawl, *Kapala* (K75-05-05), 19 Aug 1975; 1 ♂. AM P24766, east of Sydney, 33°35′S 151°59′E, 584 m, *Kapala* (K76-09-02), 24 June 1976; 1 ♀. AM P26807, north-east of Norah Head, 33°08′S 152°27′E to 33°10′S 152°24′E, 580 m, demersal prawn trawl, *Kapala* (K77-23-09), 7 Dec 1977; 10 ♂, 8 ♀. AM P25211, south-east of Broken Bay, 33°42′S 151°52′E to 33°39′S 151°54′E, 446 m, demersal prawn trawl, *Kapala* (K76-24-01), 20 Dec 1976; 1 ♂, 1 ♀. AM P33132, south-east of Wollongong, 34°31′S 151°20′E to 34°34′S 151°19′E, 684 m, demersal prawn trawl, *Kapala* (K77-21-01), 21 Nov 1977; 1 ♂. AM P33130, north-east to east of Broken Bay, 33°28′S 152°34′E to 33°36′S 152°35′E, 630 m, demersal prawn trawl, *Kapala* (K77-24-10), 14 Dec 1977; 2 juvs. AM P33135, north-east of Port Jackson, 33°47′S 151°55′E to 33°44′S 151°57′E, 806 m, demersal prawn trawl, *Kapala* (K78-26-16), 7 Dec 1978; 6 ♂, 1 ovig. ♀ cl 26.9 mm, 1 ♀. AM P33134, north-east of Point Danger, 28°03′S 154°04′E to 28°01′S 154°04′E, 724 m, demersal prawn trawl, *Kapala* (K78-23-08), 6 Nov 1978; 1 ♂. AM P33136, north-east of Jervis Bay, 34°55′S 151°13′E to 34°53′S 151°14′E, 810 m, demersal prawn trawl, *Kapala* (K78-27-05), 12 Dec 1978; 1 ♂, 2 ♀. AM P33137, north-east of North Solitary Island, 29°50′S 153°43′E to 29°48′S 153°44′E, 495 m, demersal prawn trawl, *Kapala* (K78-06-02), 25 Apr 1978; 1 ♂, 2 ovig. ♀ cl 26.1, 30.5 mm. AM P33131, east of Broken Bay, 33°32′S 152°06′E to 33°34′S 152°05′E, 820 m, demersal prawn trawl, *Kapala* (K79-20-13), 6 Dec 1979; 2 ♂. AM P21787, east of Clarence River, 29°26—20′S 153°49—50′E, 500 m, *Kapala* (K75-09-08), 12 Oct 1975; 22 ♂, 18 ♀. AM P26807, south-east of Newcastle, 33°08—10′S 152°27—24′E, 586 m, demersal trawl, *Kapala* (K77-23-09), 7 Dec 1977; 11 ♂, 7 ♀. AM P25211, east of Broken Bay, 33°43—39′S 151°52—54′E, 450 m, *Kapala* (K76-24-03), 20 Dec 1976; 1 ♂, 1 ♀. AM P24770, east of Broken Bay, 33°40—37′S 151°54—56′E, 500 m, *Kapala*, 20 July 1976; 1 ♂. AM P26810, east of Broken Bay, 33°35—33′S, 152°00—02′E, 823 m, demersal trawl, *Kapala* (K77-23-12), 8 Dec 1977; 1 ♂. AM P20999, east of Broken Bay, 33°32—38′S 152°00—04′E, 900 m, *Kapala* (K75-05-05), 19 Aug 1975; 1 ♀. AM

P24766, east of Sydney, 33°35—30′S 151°59—152°02′E, 400 m, *Kapala* (K76-09-02), 24 June 1976; 1 ovig. ♀. AM P21075, east of Broken Bay, 33°32—38′S 152°00—04′E, 900 m, *Kapala* (K75-05-05), 19 Aug 1975; 1 ♀. AM P21070, east of Broken Bay, 33°32—38′S 152°00—04′E, 900 m, *Kapala* (K75-05-05), 19 Aug 1975; 1 ♂. AM P35914, south-east of Broken Bay, 33°43′S 151°56′E to 33°39′S 151°58′E, 631 m, demersal fish trawl, *Kapala* (K84-16-03), 25 Sept 1984; 1 ovig. ♀, 3 ♀.

Diagnosis. Carapace dorsally rounded. All abdominal segments dorsally rounded. Posterior margin of telson truncate to very slightly notched. Merus of pereopod 1 unarmed; merus of pereopod 2 with 7—8 spines on posterior margin.

Description. Rostrum barely, or not reaching anterior carapace margin, directed obliquely upward, often with faint convexity on anterior margin, anteriorly usually narrowly acute, lacking any posterior carina. Carapace dorsally rounded, branchiostegal spine marginal, short unkeeled; low rounded suprabranchial ridge present. All abdominal somites dorsally rounded, lacking mid-dorsal spine

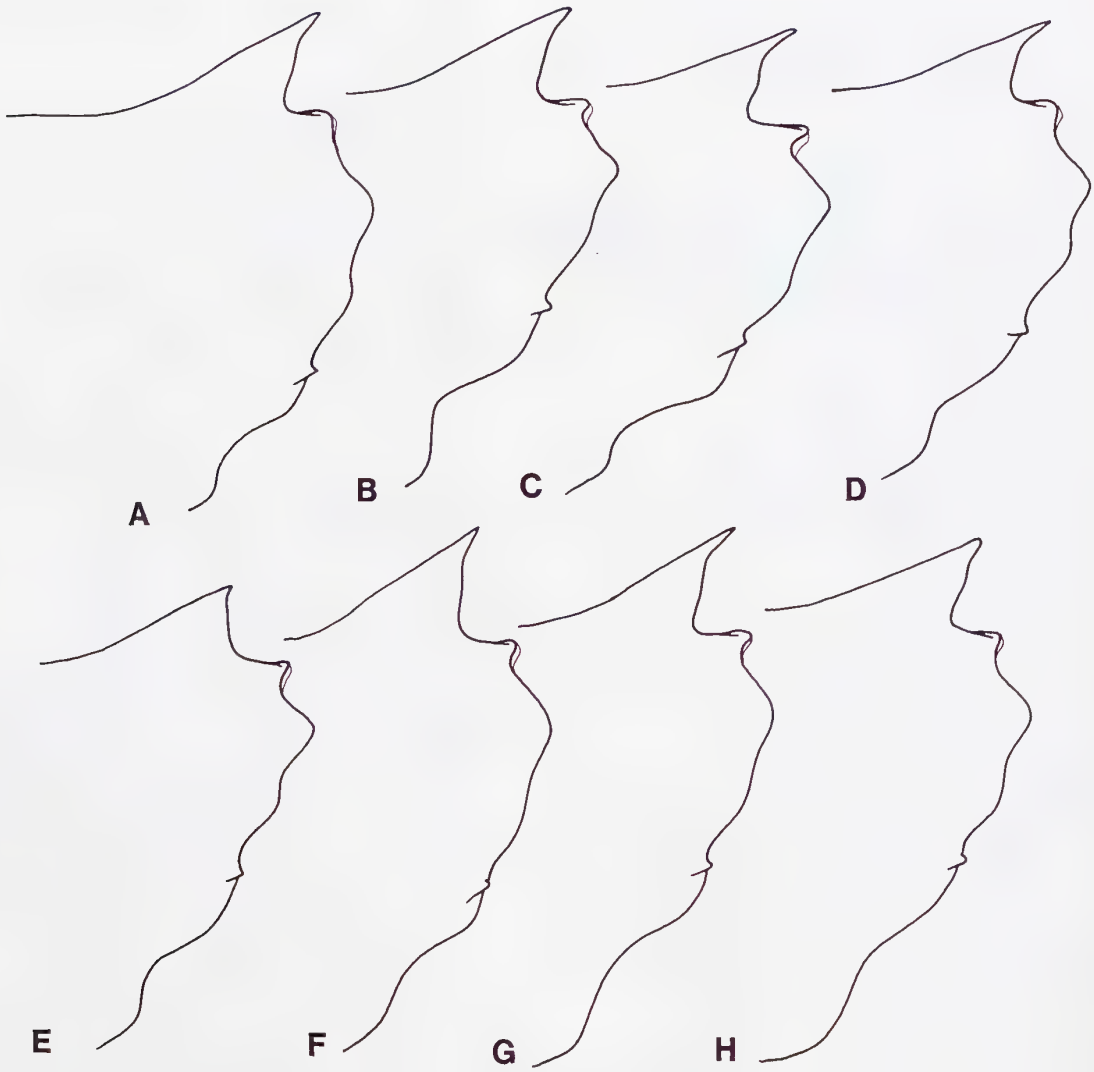

Fig. 10. *Pasiphae kapala* n.sp., anterior carapace variation. **A,** ♂ cl 24.5 mm; **B,** ♂ cl 24.0 mm; **C,** ♂ cl 23.8 mm; **D,** ♂ cl 22.6 mm; **E,** ♂ 23.0 mm; **F,** ♀ cl 24.5 mm; **G,** ♀ cl 25.0 mm; **H,** ♀ cl 22.6 mm.

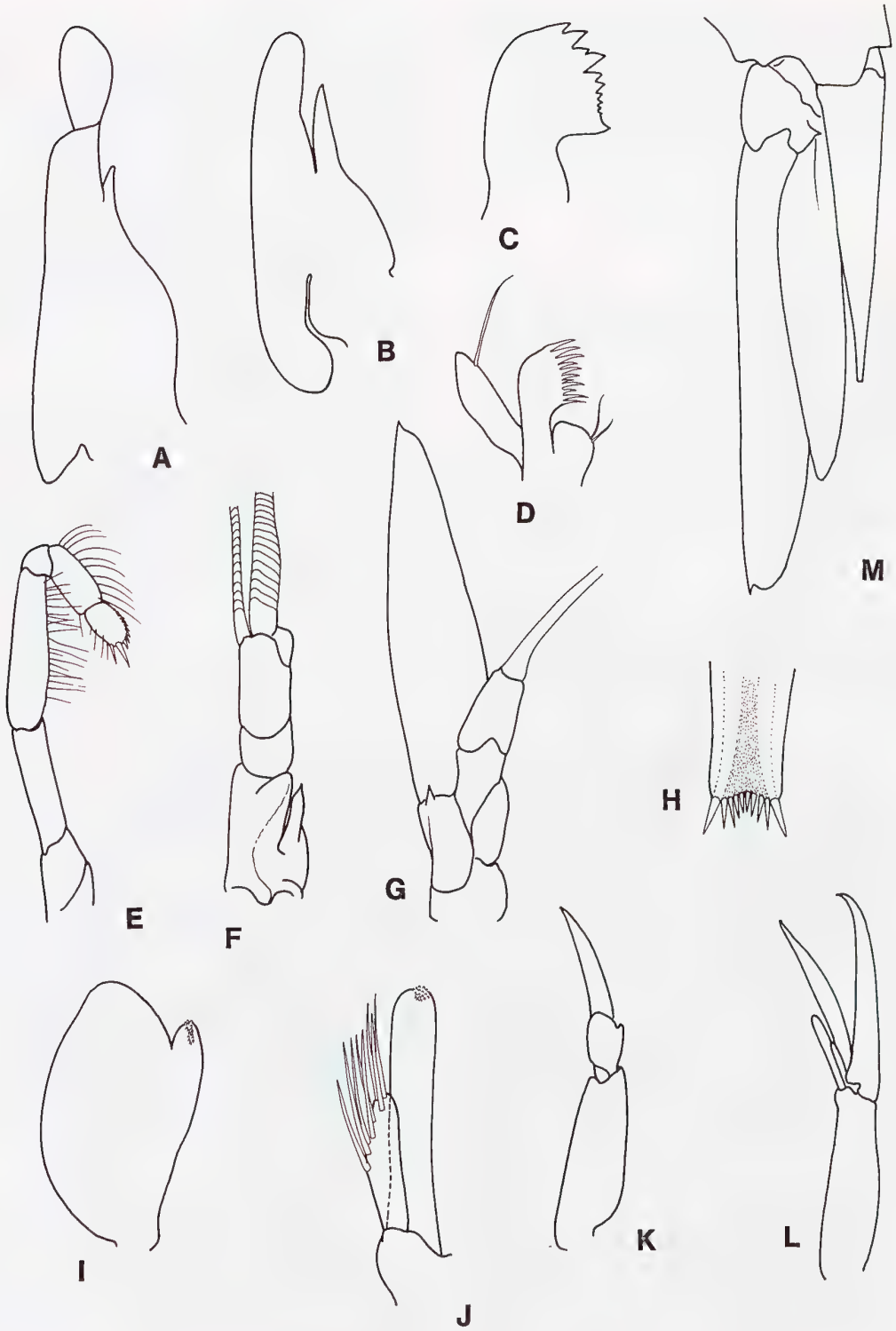

Fig. 11. *Pasiphae kapala* n.sp. **A,** maxilliped 1; **B,** maxilla 2; **C,** mandible; **D,** maxilla 1; **E,** maxilliped 3; **F,** antenna 1; **G,** antenna 2; **H,** apex of telson; **I,** pleopod 1 ♂, endopod; **J,** pleopod 2 ♂, appendix interna and appendix masculina enlarged; **K,** pleopod 1 ♂; **L,** pleopod 2 ♂.

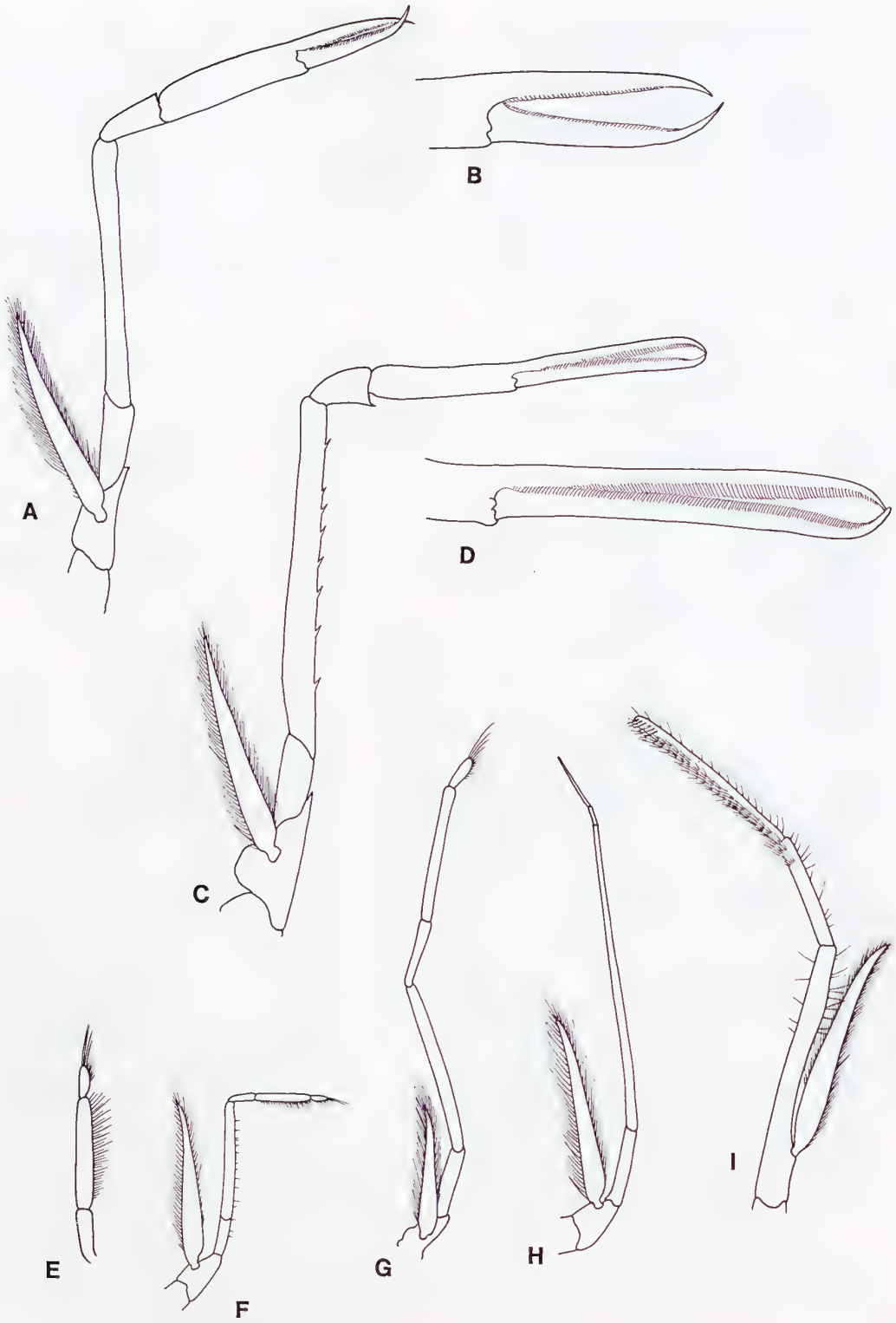

Fig. 12. *Pasiphae kapala* n.sp. **A,** pereopod 1; **B,** pereopod 1 chela enlarged; **C,** pereopod 2; **D,** pereopod 2, chela enlarged; **E,** pereopod 4, two distal articles enlarged; **F,** pereopod 4; **G,** pereopod 5; **H,** pereopod 3; **I,** maxilliped 3.

on posterior margin. Pleura of somites 1 and 2 ventrally broadly rounded; pleura of 3—5 with ventral margin almost straight, somewhat produced anteriorly into rounded lobe; somite 6, 1.4X longer than somite 5, only slightly shorter than telson. Latter with posterior margin truncate to very shallowly notched, bearing 5 pairs of spines.

Antenna 1 with stylocerite almost reaching distal margin of basal peduncular segment, twisted, distally acute; segment 2 about half length of segment 1, somewhat more than half length of segment 3.

Antenna 2, scaphocerite over-reaching antenna 1 peduncle by half its length, tapering distally to short triangular spine extending past apex of blade; peduncular segment 2 with ventrodistal spine.

Mouthparts as illustrated. Maxilliped 3 not quite reaching distal spine of scaphocerite; terminal segment slightly rounded, with row of short spines on mesial surface, single row of setae on anterior margin; posterior margin with rows of short spines; penultimate segment 0.6X length of terminal segment.

Pereopod 1 over-reaching scaphocerite by ⅔ length of fingers of chela; fingers ¾ length of palm; carpus half length of palm; merus subequal in length to chela, posterior margin unarmed.

Pereopod 2 over-reaching scaphocerite by ⅔ length of fingers of chela; fingers subequal in length to palm plus carpus; merus subequal in length to chela, with 7—8 spines on posterior margin.

Pereopod 3 very slender, reaching midlength of merus of pereopod 2; propodus ⅓ length of dactylus.

Pereopod 4 shorter than pereopods 3 or 5, reaching to distal end of carpus of pereopod 5; dactylus ovate, with setae increasing in length distally; propodus 3.5X length of dactylus, with close-set setae on posterior margin.

Pereopod 5 reaching anteriorly almost as far as distal end of pereopod 3; dactylus ovate, with setae increasing in length distally; propodus 4X length of dactylus; carpus half length of propodus.

Pleopod 1 in male with endopod roughly ovate, with rounded lobe bearing tiny hooks on mesial margin. Pleopod 2 in male with appendix masculina 0.5—0.6X length of appendix interna, bearing about 8 elongate spines on distal and outer margins; appendix interna with small patch of minute hooks on rounded apex.

Inner uropodal ramus over-reaching telsonic apex by about 0.3X its length; outer uropodal ramus over-reaching inner ramus by 0.25 of its length.

Remarks. The present species belongs to that group of species characterised by a rounded carapace and rounded abdominal somites, and a telsonic apex regarded as very faintly notched. The armature of the meri of pereopods 1 and 2 (0 and 7—8 spines respectively), however, separates this species from *P. poeyi* Chace, and *P. americana* Faxon (which has the branchiostegal spine arising posterior to the anterior margin), which have one to two spines on pereopod 2. The meral armature also separates this species from a second group of species which usually has more than 0 and 1—2 spines on pereopods 1 to 2 respectively.

Etymology. The species is named for the research vessel of the New South Wales Department of Fisheries, the FRV *Kapala.*

Distribution. Off New South Wales, 446—900 m.

Pasiphaea longitaenia n. sp.

Figs 13,14

Type material. New South Wales: HOLOTYPE: AM P35196, east of Long Reef Point, 33°43′S 151°56′E to 33°39′S 151°58′E, 626—637 m, demersal fish trawl, *Kapala* (K84-16-03), 25 Sept 1984; 1 ♂, cl 23.1 mm. PARATYPES: AM P24772, east of Broken Bay, 33°41′S 151°55′E, 457 m, demersal prawn trawl, *Kapala* (K76-24-01), 20 July 1976; 1 ♂, cl 22.3 mm, 2 ♀, cl 24.0, 26.0 mm. AM P24771, east of Broken Bay, 33°41′S 151°55′E, 457 m, demersal prawn trawl, *Kapala* (K76-24-01), 20 July 1976; 1 ♀ cl 24.1 mm (rostrum damaged). USNM 211395, east of Long Reef Point, 33°43′S 151°56′E to 33°39′S 151°58′E, 626?-637 m, demersal fish trawl, *Kapala* (K84-16-03), 25 Sept 1984; 1 ♂, cl 26.5 mm.

Diagnosis. Carapace dorsally rounded. Abdominal somites 1—5 dorsally rounded, somite 6 dorsally carinate. Telson posteriorly truncate. Merus of pereopod 1 armed with about 9 spines; merus of pereopod 2 armed with about 19 spines on posterior margin.

Description. Rostrum low, triangular, not reaching anterior carapace margin. Carapace mid-dorsally rounded; branchiostegal spine short, marginal; faint rounded suprabranchial ridge present. Abdominal somites 1—5 dorsally rounded, somite 6 subcarinate. Pleura of somites 1 and 2 ventrally broadly rounded, of 3 and 4 with rounded anteriorly directed lobes; of 5 ventrally straight, posteroventrally rectangular; somite 5 about ⅔ length of somite 6, latter ending with slight mid-dorsal spine on posterior margin. Telson ⅔ length of somite 6, with shallow mid-dorsal longitudinal groove; posterior margin truncate, bearing single median, and 4 pairs of lateral spines, outermost pair longest.

Antenna 1, basal segment with slight shoulder at about midlength of ventromesial margin; stylocerite twisted, apically acute, reaching distal margin of basal segment; segment 2 about half length of basal segment.

Antenna 2 reaching by slightly more than half length of scaphocerite blade beyond antennular peduncle; distal scaphocerite spine reaching well beyond apex of blade; second peduncular segment with distal spine at outer and at mesial distal angles.

Mouthparts as illustrated. Maxilliped 3 reaching to distal ¾ of scaphocerite, distal segment narrow, parallel-sided, apically subacute, with ventral fringe of spines, 1.6X length of penultimate segment.

Pereopod 1 reaching beyond scaphocerite by length of fingers of chela; fingers ⅔ length of palm; carpus

about ¼ length of merus; latter armed with 9—12 spines on posterior margin; basis with posterodistal margin produced into strong spine.

Pereopod 2 reaching slightly beyond fingers of pereopod 1, and by ⅔ length of fingers beyond scaphocerite; fingers subequal in length to palm; merus shorter than chela, armed with 17—19 spines on posterior margin; basis with strong posterodistal spine.

Pereopod 3 very slender, anteriorly reaching carpus of pereopod 2.

Pereopod 4 shorter than pereopods 3 or 5, reaching proximal fourth of propodus of pereopod 5; propodus 3.5X length of dactylus, with posterior fringe of spine-setae.

Pereopod 5 reaching slightly beyond midlength of merus of pereopod 3; dactylus ovate, with setae increasing in length distally; propodus 6X length of dactylus, 2.5X length of carpus; merus 3X length of carpus.

Pleopod 1 of male, endopod elongate ovate, with rounded lobe on mesial margin bearing small patch of hooks. Pleopod 2 of male with appendix masculina about ⅔ length of appendix interna, bearing 10 spines on distal and outer margins; appendix interna distally rounded, with small terminal patch of minute hooks.

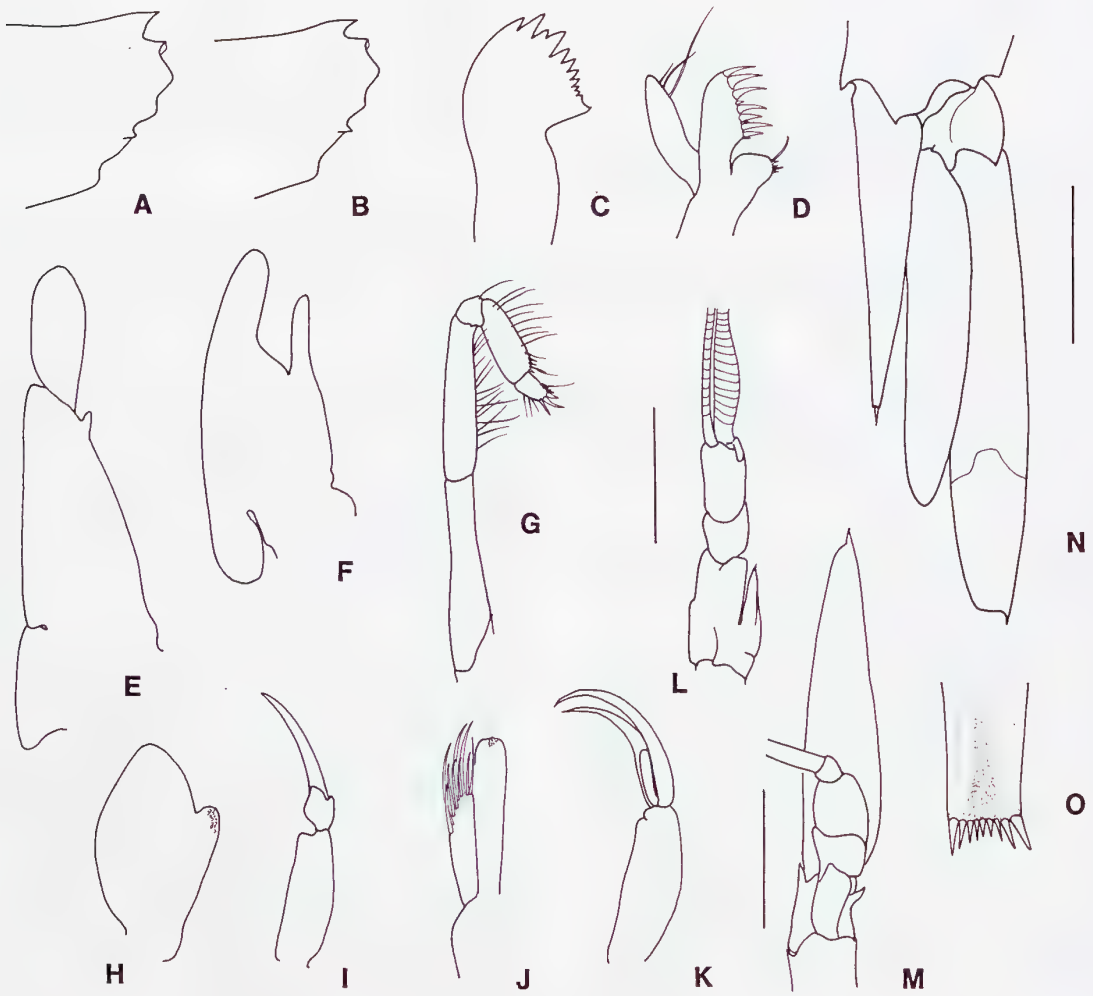

Fig. 13. *Pasiphae longitaenia* n.sp. **A,** anterior carapace, ♀ cl 26.0 mm; **B,** anterior carapace, ♀ cl 24.0 mm; **C,** mandible; **D,** maxilla 1; **E,** maxilliped 1; **F,** maxilla 2; **G,** maxilliped 3; **H,** pleopod 1 ♂, endopod; **I,** pleopod 1 ♂; **J,** pleopod 2 ♂, appendix interna and appendix masculina enlarged; **K,** pleopod 2 ♂; **L,** antenna 1; **M,** antenna 2; **N,** telson and uropod in lateral view; **O,** apex of telson. (Scales: L-N = 5 mm).

Inner uropodal ramus slightly less than ¾ length of outer ramus, over-reaching telsonic apex by about ⅓ of its length; outer ramus with truncate-rounded distal margin.

Remarks. The carapace and abdominal features of this species mentioned in the diagnosis bear some similarity to *P. truncata* Rathbun, 1906, from Hawaii. The new species may be distinguished from the latter by the following points: the rostrum is more elongate, with the anterior margin more oblique than in the Hawaiian species; abdominal somite 6 is subcarinate (narrowly rounded) in *P. longitaenia* acutely carinate in *P. truncata;* the fingers of pereopod 1 in *P. truncata* are three-fourths the length of the palm, two-thirds the length in *P. longitaenia;* the fingers of pereopod 2 are slightly longer than the palm in *P. truncata,* subequal to the palm in *P. longitaenia;* finally,the merus of pereopod 2 in *P. longitaenia* bears more spines (17—19 as against 13—16).

Etymology. The species name, the Latinised form of 'long reef', is derived from the type locality, Long Reef Point, N.S.W.

Distribution. Off New South Wales, 457—637 m.

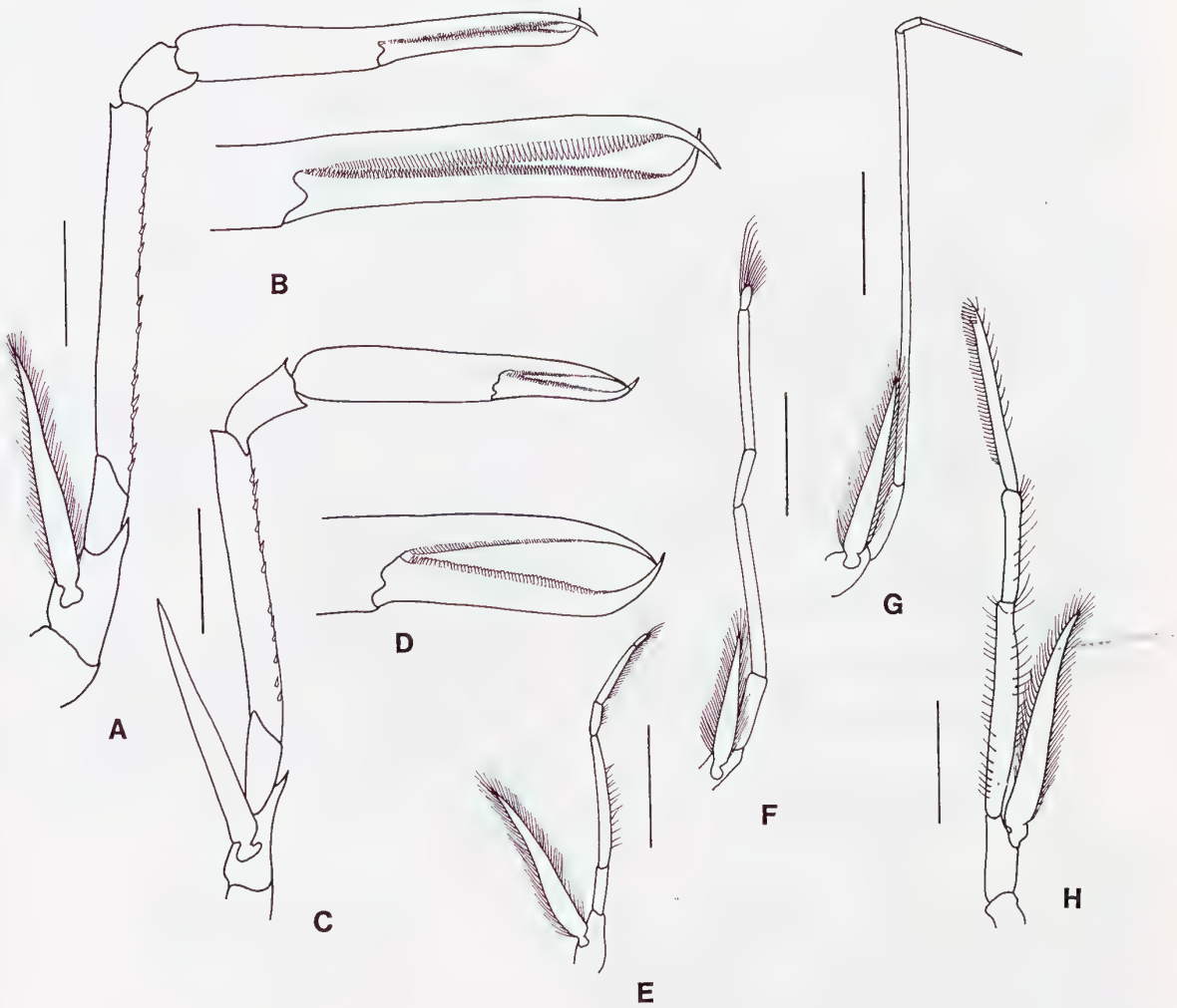

Fig. 14. *Pasiphae longitaenia* n.sp. **A,** pereopod 1; **B,** pereopod 1, chela enlarged; **C,** pereopod 2; **D,** pereopod 2, chela enlarged; **E,** pereopod 4; **F,** pereopod 5; **G,** pereopod 3; **H,** maxilliped 3. (Scales: A,C,E-H = 5 mm).

Family EUGONATONOTIDAE

Eugonatonotus Schmitt, 1926

Eugonatonotus crassus (A. Milne Edwards)

Gonatonotus crassus A. Milne Edwards, 1881: 10.—Kubo, 1937: 94—98, figs 1—3.
Eugonatonotus crassus.—Holthuis, 1955: 39—40, fig. 18; Thompson, 1966: 129—135.

Material examined. Queensland: AM P33141, north-east of Danger Point, 27°55′S 154°03′E to 27°57′S 154°03′E, 540 m, prawn trawl, *Kapala* (K78-23-09), 6 Nov 1978; 5 specimens.

Diagnosis. Rostrum subequal to carapace length, curved distally, with about 8 spines on both dorsal and ventral margins; pereopods 1 and 2 chelate, fingers of chelae short, armed with black horny spines; carpus of pereopod 2 entire; pereopods with exopods; carapace dorsally carinate with about 10 movable spines anteriorly, lateral carapace with 3 carinae; only third and fourth abdominal somites carinate, carina of third somite with spine at distal third, and pair of submedial spines on posterior margin, fourth and fifth somites with more than 2 spines on posterior margin.

Remarks. These specimens, all females (cl 34.8—38.7 mm), agree well with description and figures given by Kubo (1937). They differ in having the rostrum slightly longer (1.1—1.2) than the carapace and resembling the figure given by Kubo for the male rostrum rather than that for the female. Also, the ventral spine on the second segment of the antennal peduncle reaches a third rather than halfway along the scaphocerite, and the telson is slightly shorter, rather than subequal to the uropods. These few differences may be explained by the larger size of our specimens; in Kubo's specimens the carapace length of the largest female was 22 mm. In our specimens there are 10—12 movable spines dorsally on the carapace, while on the rostrum there are 8—10 dorsal spines and 7—8 ventral spines.

This species has not previously been recorded from eastern Australia.

Distribution. Western Pacific, western Atlantic.

Family RHYNCHOCINETIDAE

Lipkius Yaldwyn, 1960

Lipkius holthuisi Yaldwyn

Lipkius holthuisi Yaldwyn, 1960: 16, figs 1—16.—Thompson, 1966: 129, 130, 136, 138.

Material examined. New South Wales: AM P21000, east of Broken Bay, 33°32′S 152°04′E to 33°38′S 152°00′E, 810 m, demersal prawn trawl, *Kapala* (K75-05-05), 19 Aug 1975; 1 ♀ cl 32.5 mm (rostrum damaged). AM P26559, east of Broken Bay, 33°35′S 152°01′E to 333°32′S 152°03′E, 810 m, demersal prawn trawl, *Kapala* (K76-24-03), 20 Dec 1976; 1 ♀ cl 33.2 mm (rostrum damaged).

Diagnosis. Rostrum long, slender, immovable, armed with movable teeth proximally, more widely spaced fixed teeth distally. Carapace lacking carinae. Rudimentary exopods on pereopods 1—3. Anteriorly projecting, ventral, bifid plate between bases of pereopods 2—5.

Distribution. Cook Strait to Chatham Rise, New South Wales; 400—810 m.

Family CAMPYLONOTIDAE

Campylonotus Bate, 1888

Campylonotus rathbunae Schmitt

Campylonotus rathbunae Schmitt, 1926: 373—377, pl. 67, figs 1—5.—Yaldwyn, 1960: 20—27, figs 2—4.

Material examined. New South Wales: AM P19093, east of Long Reef, 33°51′S 151°51′E to 33°45′S 151°55′E, 675 m, trawl, *Kapala* (K72-06-03), 19 Oct 1972; 1 specimen. AM P24774, east of Brush Island, 35°28′S 150°50′E to 35°33′S 150°47′E, 567—594 m, fish trawl, *Kapala* (K76-11-12), 8 July 1976; 1 ovig. ♀. Victoria: AM P33142, south-east of Gabo Island, 37°48′S 150°13′E to 37°45′S 150°15′E, 486 m, fishtrawl, *Kapala* (K77-10-08), 13 July 1977; 1 ovig. ♀. AM P20802, south-east of Gabo Island, 37°36′S 150°17′E to 37°43′S 150°15′E, 540 m, fish trawl, *Kapala* (K75-03-04), 11 July 1975; 1 ovig. ♀. AM P33143, P26803, south-east of Gabo Island, 37°43′S 150°17′E to 37°40′S 150°17′E, 630 m, prawn trawl, *Kapala* (K77-22-04), 30 Nov 1977; 24 specimens. Western Australia: AM P21956, Great Australian Bight, 33°28′S 127°15′E to 33°31′S 127°19′E, 640—650 m, otter trawl, J.R. Paxton on *Dmitry Mendeleev*, 28 Feb 1976; 7 specimens.

Diagnosis. Rostrum narrow with 2 large basal teeth, first of which standing at or behind middle of carapace, ventral margin of rostrum with 3—4 teeth; pereopods 1 and 2 chelate; pereopod 2 subequal, carpus entire; pereopods without exopods. Carapace with 2 lateral carinae. Abdomen armed with posterior dorsal spines on segments 3—5, and on anterior part of third segment by prominent tubercle, segments 1, 2, and 6 without carinae.

Remarks. This species has been figured and described in detail by Yaldwyn (1960). The only previous record from Australian waters was from the Great Australian Bight (Schmitt, 1926).

These specimens were collected between 33°S and 38°S and between 127°E and 150°E in trawls at depths to 650 m.

Distribution. Southern and southeast Australia, southeast New Zealand; 400—650 m.

Family HIPPOLYTIDAE

Lebbeus White, 1847

Lebbeus yaldwyni n. sp.

Figs 15—17

Type material. New South Wales: HOLOTYPE: AM P26561, east of Sydney, 33°43′S 151°51—53′E, 450 m, *Kapala* (K77-04-13), 6 May 1977; 1 ovig. ♀, cl 11.5 mm.

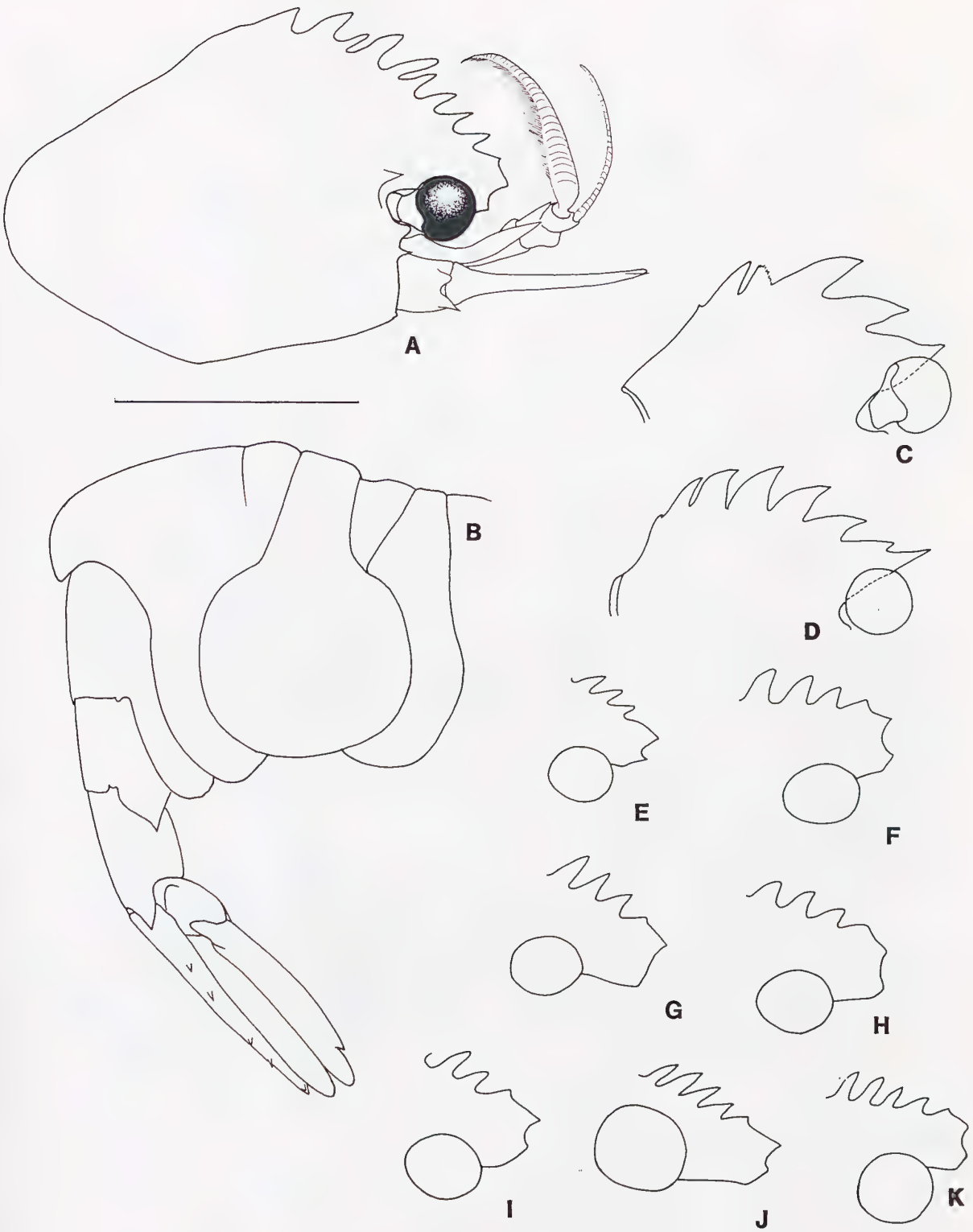

Fig. 15. *Lebbeus yaldwyni* n.sp. **A,** carapace in lateral view; **B,** abdomen in lateral view. *Lebbeus compressus* Holthuis: **C,** dorsal carapace of holotype; **D,** Specimen from Tosa, Japan, cl 8.9 mm. Rostral variation in L. yaldwyni n.sp. **E-I,** AM P26840; **J,** AM P24769; **K,** AM P26561. (Scales: A,B = 10 mm).

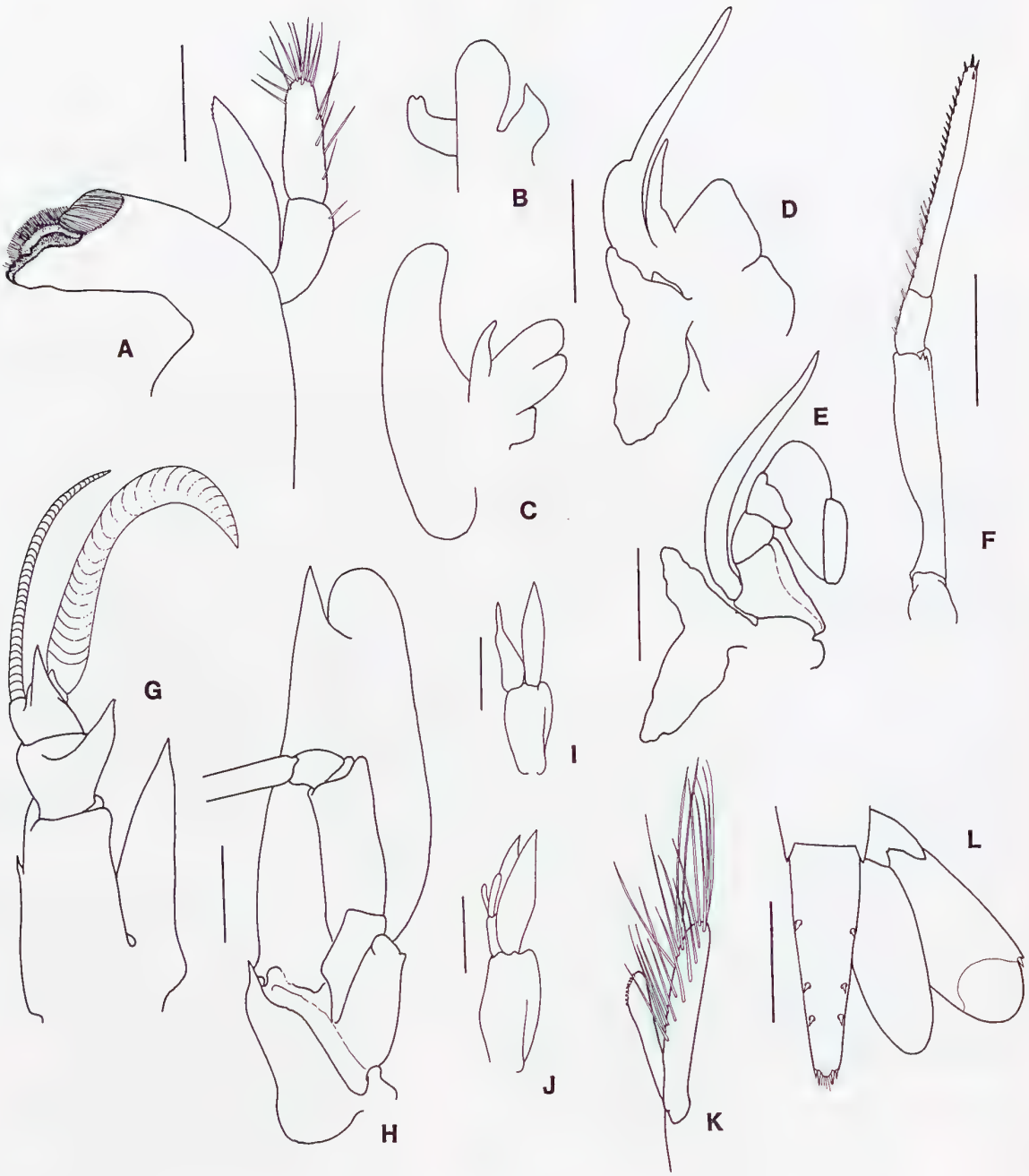

Fig. 16. *Lebbeus yaldwyni* n.sp. **A,** mandible; **B,** maxilla 1; **C,** maxilla 2; **D,** maxilliped 1; **E,** maxilliped 2; **F,** maxilliped 3; **G,** antenna 1; **H,** antenna 2; **I,** pleopod 1 ♂; **J,** pleopod 2 ♂; **K,** pleopod 2 ♂, appendix interna and appendix masculina enlarged; **L,** telson and right uropod. (Scales: A-E = 1 mm, F = 5 mm, G,H = 2 mm, I,J = 3 mm, L = 5 mm).

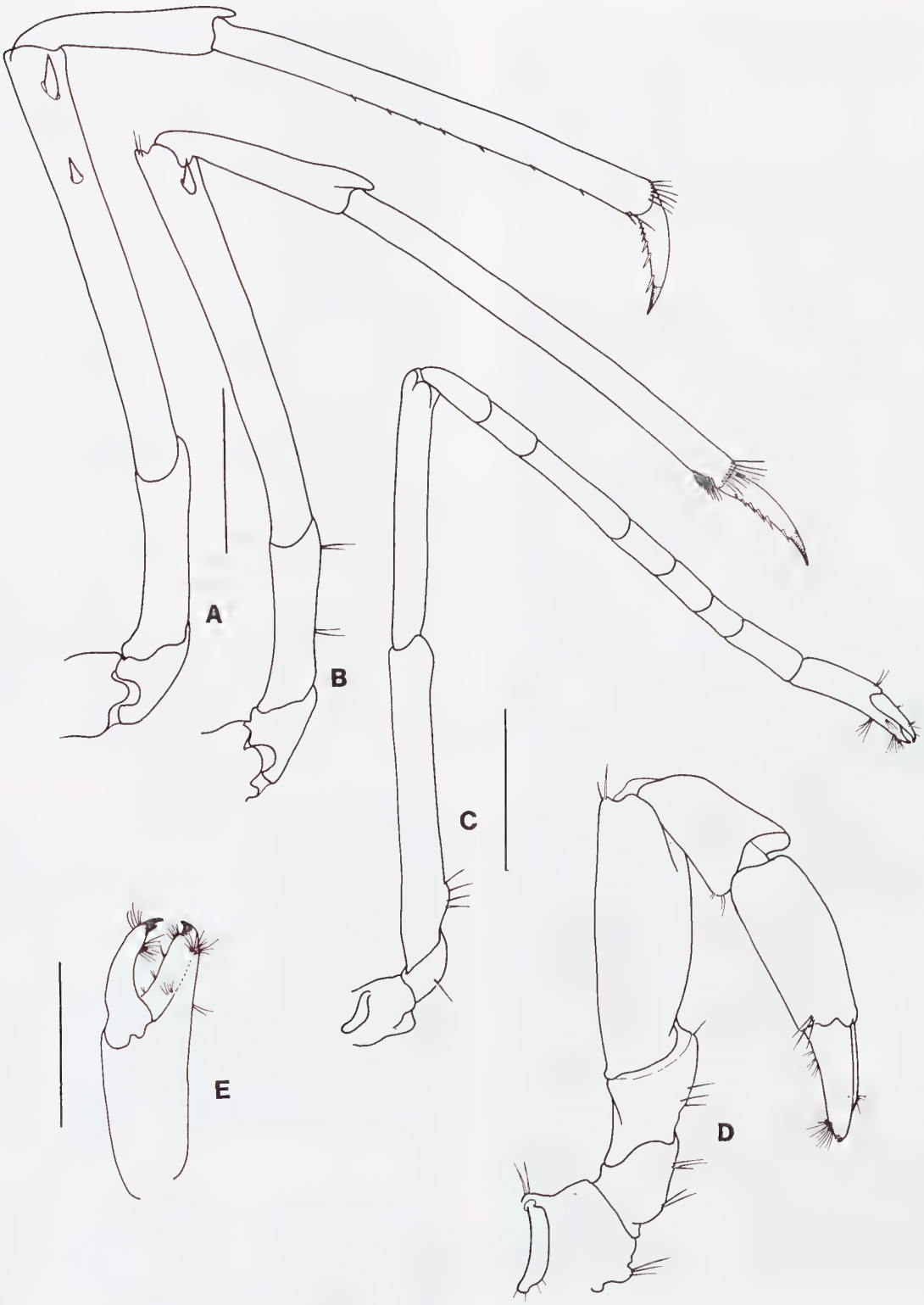

Fig. 17. *Lebbeus yaldwyni* n.sp. **A,** pereopod 3; **B,** pereopod 5; **C,** pereopod 2; **D,** pereopod 1; **E,** chela of pereopod 1. (Scales: A-E = 3 mm).

PARATYPES: AM P33109, east of Sydney, 33°43′S 151°51—53′E, 450 m, *Kapala* (K77-04-13), 6 May 1977; 1 ovig. ♀, cl 11.7 mm. AM P24769, east of Batemans Bay, 34°44′S 150°37′E to 35°47′S 150°35′E, 420 m, *Kapala* (K76-11-08), 7 July 1976; 1 ♂, cl 5.1 mm. AM P21825, east of Sydney, 33°51′S 151°45′E to 33°47′S 151°48′E, 470 m, *Kapala* (K75-12-01), 11 Dec 1975; 1 ♀, cl 7.8 mm. AM P26840, east of Brush Island, 35°31′S 150°45—47′E, 190 m, demersal prawn trawl, *Kapala* (K77-21-04), 22 Nov 1977; 5 ♀, cl 8.5—11.6 mm. USNM 221396, east of Brush Island, 35°31′S 150°45—47′E, 190 m, *Kapala* (K77-21-04), 22 Nov 1977; 2 ♀, cl 11.0—11.3 mm.

Diagnosis. Carapace high-crested, dentate to posterior margin; rostrum a continuation of carapace crest, broad anterior to eye, apically variable from truncate-concave to acutely triangular, but reaching only short distance anterior to eye. Antennal, supraorbital, and pterygostomian spine present, branchiostegal spine absent. Abdominal somites dorsally rounded. Mandibular palp of 2 articles. Maxilliped 3 lacking exopod. Pereopod 2, carpus of 7 articles. Pereopods lacking arthrobranchs.

Description. Carapace with broad dentate mid-dorsal crest extending almost from posterior margin onto rostrum, sloping anteroventrally; rostral-postrostral tooth count: 9—11/0—1. Rostrum variable, anteriorly obliquely truncate or hollowed, reaching almost to distal margin of basal antennular article. Carapace with single strong marginal supraorbital spine, marginal antennal spine, pterygostomian angle with rounded papilla (not quite a spine); lateral carapace with faint hepatic groove; low rounded suprabranchial ridge present.

All abdominal somites dorsally rounded. Pleura of somites 1—4 ventrally rounded, of somite 2 subcircular, of somite 4 elongate-oval; posteroventral angle of pleuron 5 acute. Somite 3 dorsally strongly hooded and curved, with rounded mid-dorsal suggestion of ridge in posterior three-fourths. Somite 5 ¾ length of somite 6. Latter with almost rectangular posteroventral corner; lobe overlapping lateral base of telson acute-spinose. Telson dorsally gently convex, with 3—5 pairs of dorsolateral spines, tapering to convex posterior margin bearing short outer, and longer inner pair of spines, with several fine setae between longer pair of spines.

Cornea of eye much wider than eyestalk, well pigmented.

Antennular stylocerite lanceolate, distally acute, extending well beyond distal margin of basal peduncular article. Distal margin of basal article bearing row of plumose setae; mesial margin with spine at distal two-thirds; second article with strong triangular spine at outer distal angle; third article with strong triangular spine directed anteriorly; inner flagellum slender, shorter than ventral flagellum; latter robust, tapering distally, of about 20 setigerous articles.

Antennal scaphocerite with outer margin almost straight, ending strong spine not extending beyond rounded distal margin of blade; latter widest at proximal third; basal antennal article bearing strong ventral spine; flagellum extending posteriorly to level of third abdominal somite.

Mandibular palp of 2 articles, distal setose article slightly longer than proximal article; incisor flattened, slender, tapering to acute apex, bearing 4 or 5 fine distal serrations; molar stout, grinding surface oblique-truncate.

Maxilla 1, maxilla 2, maxilliped 1, and maxilliped 2 as figured.

Maxilliped 3 extending beyond scaphocerite by half length of distal article, distal article flattened, parallel-sided for most of its length, with single row of 19—20 corneous spines on mesial margin.

Pereopod 1 reaching distal ⅔ of scaphocerite, robust, fingers slightly shorter than palm; corneous acute tip of fixed finger fitting between 2 corneous apical spines of dactyl.

Pereopod 2 extending beyond scaphocerite by length of chela; carpus almost 1.75X length of merus, composed of 7 articles; ischium slightly longer than merus.

Pereopod 3 over-reaching scaphocerite by half length of propodus plus dactyl; dactyl with corneous apical spine and 6 smaller spines on flexor margin; propodus with 5 or 6 spines on distal half of flexor margin; carpus slightly less than half length of propodus, unarmed; merus with distal spine on outer surface, smaller spine at about distal two-thirds.

Pereopods 4 and 5 each extending anteriorly slightly less than pereopod 3, of similar proportions to pereopod 3, each with single distal spine on outer surface of merus.

Pereopods 1—5 each with single pleurobranch; epipod present on pereopods 1 and 2.

Uropodal basis with outer distal lobe apically narrowly rounded; outer ramus slightly longer than inner, with fixed marginal tooth and movable spine at about distal three-fourths.

Colour. Carapace with 4—6 curved lateral scarlet stripes running from ventral margin onto rostral-postrostral crest; latter with few additional stripes or blotches. Abdominal pleuron 1 with 3 broad bands; pleuron 2 with 2 bands; pleuron 3 with 1 band; somite 1 and 2 with single band running from pleuron; somite 3 with 3 bands. Remainder of abdomen pale pink-white. Bases of antennae, maxilliped 3, pereopod 1 up to carpus, and pereopods 2—5 bases orange red; distal articles of appendages transparent pink.

Remarks. From Holthuis' discussion (1947) of the species of *Lebbeus,* and Wicksten & Méndez' (1982) key to the eastern Pacific species, the present material would belong to the group possessing epipods on the first two pairs of pereopods. This group includes *L. brandtii* (Brazhnikov, 1907), *L. grandimanus* (Brazhnikov, 1907), *L. polaris* (Sabine, 1824) (= *L. unalaskensis* Rathbun, 1902), *L. scrippsi*

Wicksten & Méndez, 1982, and *L. splendidus* Wicksten & Méndez, 1982.

Lebbeus polaris (Sabine) possesses a more elongate rostrum than the present species, and does not have a high-crested carapace. *Lebbeus brandtii* (Brazhnikov) has a short rostrum lacking, or with only one ventral tooth. *Lebbeus grandimanus* (Brazhnikov) has a relatively narrow rostrum, seen in lateral view, with four postorbital teeth not forming a crest. The two eastern Pacific species, *L. scrippsi* and *L. splendidus* Wicksten & Méndez both have narrow non-crested rostra with few dorsal teeth.

Lebbeus compressus Holthuis, 1947 (= *Spirontocaris gibberosa* Yokoya, 1933), a species possessing a toothed and crested carapace, has epipods on pereopod 1 only. (The holotypic male of this species, from 232 m at Siwoya-Zaki, Japan, was examined. Having a carapace length of 4.8 mm, the specimen probably dried out at some stage, and the carapace was damaged. It is possible that the epipod of pereopod 2 has been lost on both sides, because of this poor condition, but this seems unlikely). While Yokoya (1933) stated that the rostrum of his holotype was "broken off", there is no sign of damage in the rostral area. In fact, the rostrum is an acutely triangular, forwardly directed spine, quite unlike the present species.

Etymology. The species is named for Dr John Yaldwyn, director of the National Museum of New Zealand, and eminent carcinologist.

Merhippolyte Bate, 1888

Merhippolyte chacei n. sp.

Figs 18,19

Type material. New South Wales: HOLOTYPE: AM P19092, 33°43—37'S 151°55'—152°02'E, 686 m, bottom trawl, *Kapala* (K72-06-04), 19 Oct 1972; 1 ♀, cl 13.2 mm, (tip of rostrum damaged).

Additional material examined. AM P25038, east of Brush Island, 35°41—44'S 150°38—40'E, 549 m, *Kapala* (K76-19-04), 10 Nov 1976; 1 ♀, cl 9.5 mm.

Diagnosis. Rostrum almost 1.5X length of carapace, with 4—5 dorsal teeth, 7 ventral teeth, deepest just anterior to eye, anterior half dorsally unarmed. Pterygostomian angle rounded. Pleuron of abdominal somite 4 with small posteroventral tooth. Ocellus largely fused with cornea of eye. Epipods present on pereopods 1—4. Pereopod 2 reaching well beyond scaphocerite.

Description. Rostrum almost 1.5X carapace length, broadest just anterior to eye, anterior half dorsally unarmed, upswept, apex bifid; formula: 4—5/7; 2 postorbital spines present. Carapace with strong antennal spine; pterygostomian angle rounded. All abdominal somites dorsally rounded; pleura of somites 1—3 ventrally rounded; pleuron 4 broad, with small but distinct posteroventral tooth; pleuron 5 acute, triangular; somite 5 half length of somite 6; posteroventral angle of somite 6 with small tooth; posterolateral lobe overlapping telsonic base triangular, acute. Telson dorsally gently convex, with 2 pairs dorsolateral spines in posterior half; posterior margin broadly triangular, with 3 pairs of spines, second pair longest.

Cornea of eye much wider than eyestalk, well pigmented; dorsal ocellus half fused to cornea.

Antennular stylocerite lanceolate, with small basal tooth on outer margin, reaching distal margin of basal antennular peduncle article; small tooth on ventromesial margin at about distal two-thirds; second and third peduncular articles unarmed; dorsal flagellum subequal to carapace and rostrum in length; ventral flagellum somewhat longer.

Antennal scaphocerite with outer margin straight, distal spine not reaching rounded apex of blade; basal segment with small ventrodistal tooth; blade over-reaching antennular peduncle by about half its length.

Mandibular palp of 3 setose articles, second article broadest; incisor flattened, tapering, with 5 faint distal serrations; molar robust, distally obliquely truncate.

Maxilla 1, maxilla 2, maxilliped 1, and maxilliped 2 as figured.

Maxilliped 3 just over-reaching antennal blade; distal article strongly setose-spinose.

Epipods present on pereopods 1—4. Pereopod 1 reaching distal third of scaphocerite, shorter but more robust than following pereopods; fingers slightly shorter than palm; chela subequal in length to carpus; ischium produced on flexor margin into distally acute setose blade-like crest; basis with less conspicuous extension of flexor margin. Pereopod 2 over-reaching scaphocerite by distal third of carpus plus chela; fingers slightly shorter than palm; carpus consisting of 14 articles. Pereopods 3—5 similar, dactyls with strong distal corneous spine and 7 shorter spines on flexor margin; merus with 3 articulated spines on outer surface.

Uropodal basis with acute lobe overlapping outer ramus; latter extending slightly beyond inner ramus and telsonic apex, with fixed and articulated spine on outer margin at about distal three-fourths.

Remarks. Crosnier & Forest (1973) summarise the main differences between the five species of *Merhippolyte* described to that date. Taking the present species and working through the features listed in their Table 6, it can be seen that *M. chacei* differs from all the earlier species in several respects. The rostral formula of 4—5/7 is distinctive. The rounded pterygostomian angle only resembles *M. americana* Holthuis, 1961, and *M. kauaiensis* (Rathbun, 1906). The fourth abdominal pleuron only resembles that of *M. agulhasensis* Bate, 1888.The ocellus being largely fused with the cornea resembles *A. americana* and *M. ancistrota* Crosnier & Forest. Epipods on pereopods 1 to 4 are seen in *M. agulhasensis* and *M. calmani* Kemp & Sewell, 1912.

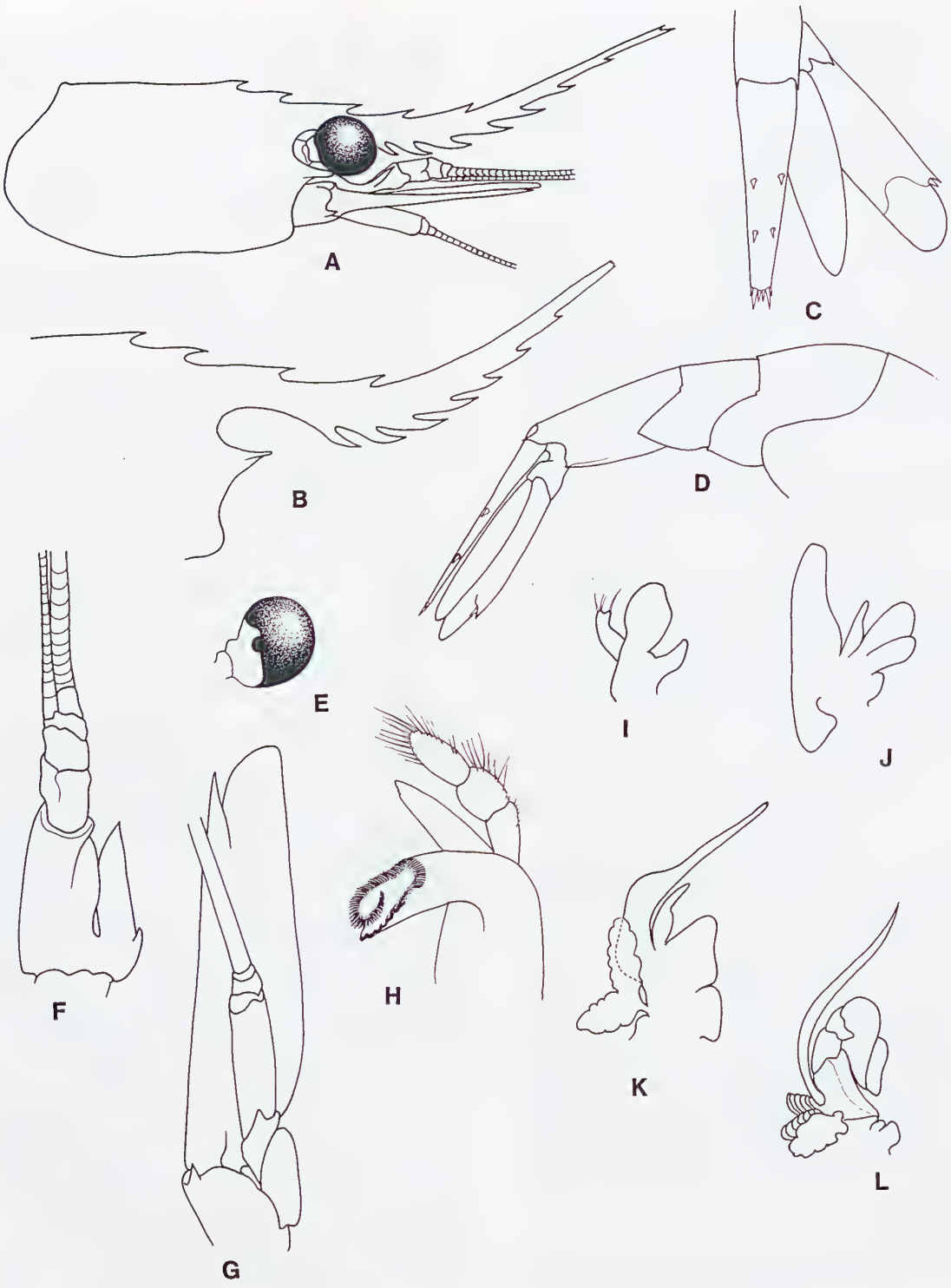

Fig. 18. *Merhippolyte chacei* n.sp. **A,** paratype in lateral view; **B,** rostrum of holotype; **C,** telson and uropod in dorsal view; **D,** abdominal somites 4–6 and tailfan in lateral view; **E,** eye; **F,** antenna 1; **G,** antenna 2; **H,** mandible; **I,** maxilla 1; **J,** maxilla 2; **K,** maxilliped 1; **L,** maxilliped 2.

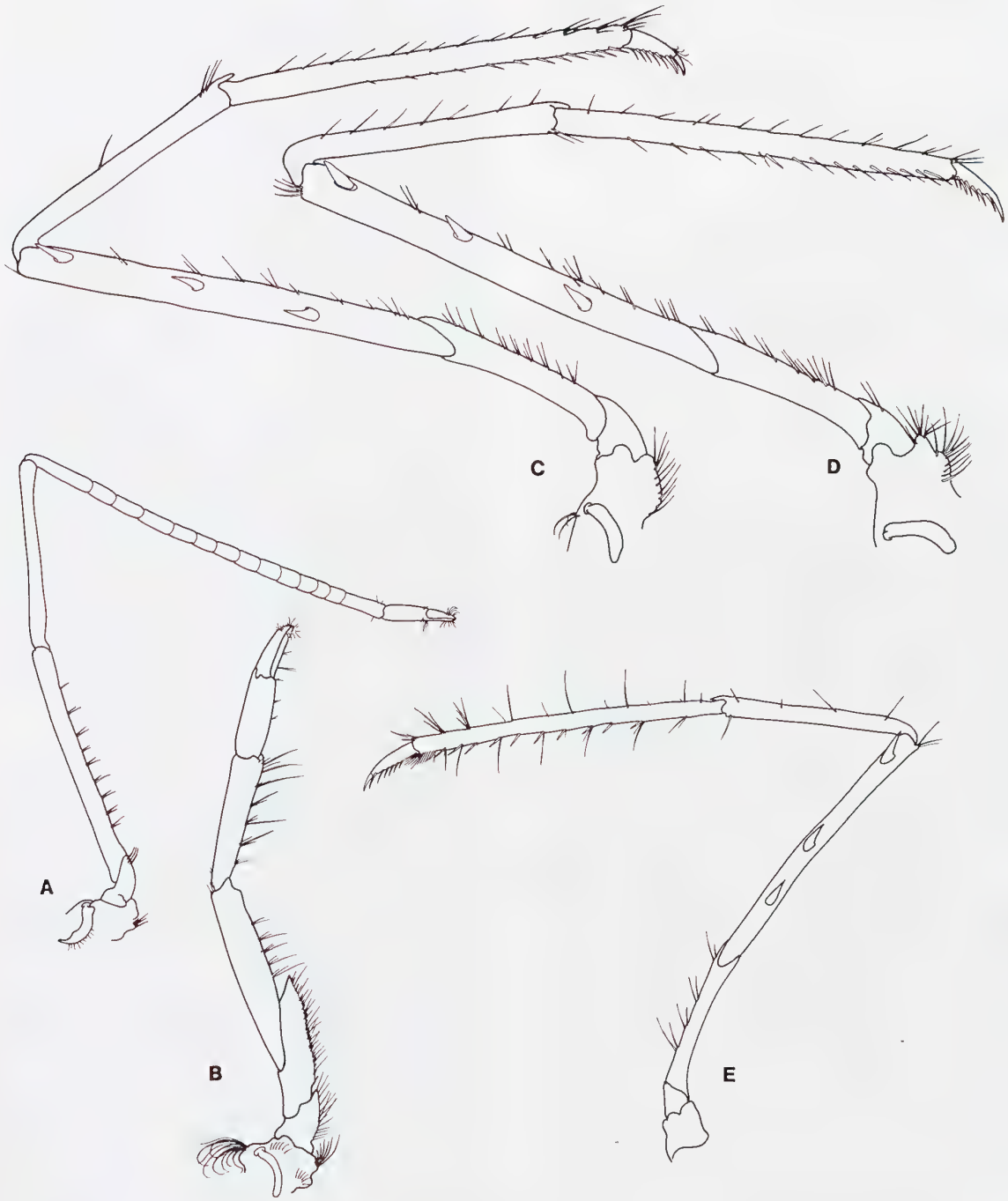

Fig. 19. *Merhippolyte chacei* n.sp. **A**, pereopod 2; **B**, pereopod 1; **C**, pereopod 4; **D**, pereopod 3; **E**, pereopod 5.

Further differences include the deeper rostral shape than that seen in *M. agulhasensis,* the ventrally produced ischium of pereopod 1, not seen in *M. calmani,* and pereopod 2 extending well beyond the scaphocerite, unlike *M. kauaiensis* where pereopod 2 is shorter than the scaphocerite by the length of the chela.

Etymology. The species is named for Fenner A. Chace, Jr. of the Smithsonian Institution, whose contributions to shrimp taxonomy are of inestimable value.

Family PANDALIDAE

Chlorotocus A. Milne Edwards, 1882

Chlorotocus novaezealandiae (Borradaile)

Thalassocaris novae-zealandiae Borradaile, 1916: 84, fig. 2.
Chlorotocus novaezealandiae.—Crosnier & Forest, 1973: 186; Chace, 1985: 11.

Material examined. New South Wales: AM P32492, north-east of Batemans Bay, 35°28—26′S 150°44—43′E, 40 m, trawl, *Kapala* (K76-01-03/04), 25 Mar 1976; 28 specimens (12 ovig. ♀).

Diagnosis. Rostrum just falling short of, just reaching, or just extending beyond, third antennular peduncle article; slender, with dorsal and ventral teeth (10—13/3—5). Carapace lacking lateral carinae; with antennal and branchiostegal spine. Pleuron of abdominal somite 5 with small posteroventral tooth. Somite 6 with short submarginal posteroventral tooth. Pereopods 1—4 each with epipod. Pereopod 1 not reaching scaphocerite apex. Pereopod 2, legs subequal, similar; chela with gape, dactylus with proximal lobe on 'cutting' margin; carpus of 2 articles.

Remarks. *Chlorotocus novaezealandiae* differs from the very similar and very widespread *C. crassicornis* (Costa) in two major characters: the rostrum (just reaching or barely over-reaching the distal antennular peduncle article in *C. novaezealandiae,* reaching well beyond in *C. crassicornis),* and size (ovigerous females of *C. novaezealandiae* 10.8—14.0 mm; of *C. crassicornis* 16.5—20.0 mm). The distribution of the anterior rostral teeth provides a subtle feature, becoming obsolete and close-set in the New Zealand species, but being evenly spaced in the more widespread species.

This is the first record of the species outside New Zealand waters.

Distribution. New Zealand; New South Wales; 140 m.

Heterocarpus A. Milne Edwards, 1881

Heterocarpus sibogae de Man

Heterocarpus ensifer Bate, 1888: 638—640, pl. 112, fig. 4.—Alcock, 1901: 107. (Not *Heterocarpus ensifer* A. Milne Edwards, 1881.)

Heterocarpus sibogae de Man, 1917: 283—284; 1920: 156, 169—171, pl. 14, figs 42—44.—Schmitt, 1926: 380—381; Calman, 1939: 206; Crosnier & Forest, 1973: 191—192 (in discussion); Chace, 1985: 36, figs 13m, 18—20.

Material examined. Queensland: AM P25147, east of Fraser Is., 36O m, *Markwell Enterprise,* Jan 1977; 7 specimens (4 ovig. ♀). AM P33025, north-east of Danger Point, 27°55′S 154°03′E to 27°57′S 154°03′E, 540 m, prawn trawl, *Kapala* (K78-23-09), 6 Nov 1978; 4 specimens (1 ovig. ♀). AM P33211, north-east of Danger Point, 28°01′S 154°00′E to 27°58′S 154°00′E, 540 m, prawn trawl, *Kapala* (K78-17-10), 17 Aug 1978; 10 specimens (1 ovig. ♀). AM P33026, north-east of Danger Point, 28°02′S 153°59′E to 27°59′S 153°59′E, 540 m, prawn trawl, *Kapala* (K78-09-05), 2 June 1978; 41 specimens (7 ovig. ♀). New South Wales: AM P33027, east of mouth of Clarence River, 29°41′S 153°45′E to 29°32′S 153°47′E, 405 m, prawn trawl, *Kapala* (K75-09-04), 10 Oct 1975; 4 specimens (3 ovig. ♀). AM P33028, north-east of Solitary Island, 29°47′S 153°44′E to 29°49′S 153°43′E, 432 m, prawn trawl, *Kapala* (K78-16-07), 2 Aug 1978; 14 specimens (5 ovig. ♀). AM P17906, north-east of Coffs Harbour, 29°49′S 153°42′E to 29°59′S 153°38′E, 369 m, prawn trawl, *Kapala* (K71-09-04), 12 May 1971; 4 specimens (2 ovig. ♀). AM P33208, north-east of North Solitary Island, 29°51′S 153°42′E to 29°55′S 153°42′E, 405 m, prawn trawl, *Kapala* (K78-06-06), 26 Apr 1978; 17 specimens (6 ovig. ♀). AM P26575, east of Wooli, 29°52′S 153°43′E to 29°51′S 153°43′E, 495 m, trawl, *Kapala* (K77-13-10), 23 Aug 1977; 18 specimens (4 ovig. ♀). AM P33209, north-east of North Solitary Island, 29°56′S 153°43′E to 29°53′S 153°41′E, 360 m, prawn trawl, *Kapala* (K78-06-01) 25 Apr 1978; 5 specimens (1 ovig. ♀). AM P19639, offshore between Newcastle and Sydney, 33°00′S 152°31′E to 33°44′S 151°50′E, 360—351 m, trawl, *Kapala,* July 1972; 1 specimen. AM P17905, east of Sydney, 33°39′S 152°55′E to 33°50′S 152°46′E, 360 m, trawl, *Kapala* (K71-05-04), 6 Apr 1971; 3 specimens. AM P33210, east of Sydney, 33°41′S 151°53′E to 33°39′S 151°56′E, 477 m, prawn trawl, *Kapala* (K80-21-05), 16 Dec 1980; 4 specimens. AM P25207, east of Sydney, 33°43′S 151°52′E to 33°39′S 151°54′E, 441—453 m, trawl, *Kapala* (K76-24-01), 20 Dec 1976; 5 specimens. AM P33032, east of Sydney, 33°46′S 151°49′E to 33°44′S 151°51′E, 432—418 m, prawn trawl, *Kapala* (K80-21-04), 16 Dec 1980; 1 specimen. AM P19094, east of Sydney, 33°51′S 151°51′E to 33°45′S 151°55′E, 675 m, prawn trawl, *Kapala* (K72-O6-03), 19 Oct 1972; 1 specimen. AM P21040, P21047, north-east of Wollongong, 34°16′S 151°26′E to 34°22′S 151°23′E, 360 m, prawn trawl, *Kapala* (K75-05-01), 8 Aug 1975; 5 specimens (1 ovig. ♀). AM P21054, north-east of Wollongong, 34°21′S 151°24′E to 34°14′S 151°28′E, 396 m, prawn trawl, *Kapala* (K75-05-02), 8 Aug 1975; 13 specimens (3 ovig. ♀). AM P33029, north-east of Wollongong, 34°21′S 151°23′E to 34°19′S 151°25′E, 432 m, demersal trawl, *Kapala* (K78-27-13), 13 Dec 1978; 6 specimens (1 ovig. ♀). AM P33030, east of Port Kembla, 34°28′S 151°19′E to 34°34′S 151°17′E, 405 m, prawn trawl, *Kapala* (K75-05-07), 20 Aug 1975; 2 specimens (1 ovig. ♀). AM P33031, east of Shoalhaven Bight, 34°50′S 151°15′E, 828 m, dredge, *Kapala* (K78-27-04), 12 Dec 1978; 1 specimen.

Diagnosis. Rostrum about equal to carapace length in adult, with 9—26 dorsal and 6—13 ventral

spines. Postrostral crest starting about halfway along carapace. Carapace with strong antennal, lateral, and posterior intermediate keels. Abdominal somites 2—4 strongly carinate, somites 3 and 4 with strong posterior dorsal spine. First pair of pereopods lacking chelae; second pair of pereopods markedly unequal, carpus consisting of 6—11 articles in shorter, 17—30 in longer.

Remarks. *Heterocarpus sibogae* is distinguished from the very similar *H. ensifer* A. Milne Edwards by the carination of the abdominal somites. In all the specimens in this series there is, on the second abdominal segment, a high carina which often projects anteriorly and is subacute at its posterior angle. There is a less pronounced carina on the posterior half of the first segment and a ridge anteriorly. We have examined specimens of *H. ensifer* (AM P9865) from Hawaii and they have only a very low indistinct ridge on both the first and second abdominal segments.

In large specimens, including ovigerous females, the rostrum is usually 0.8 to 1.1 times the carapace length while in smaller specimens (cl 17—19 mm) the rostrum is 1.3 to 1.4 times the carapace length. The rostral formula varies from 12/7 to 18/10 in the Australian material.

The species was previously recorded from southwest of Gabo Island, Victoria, by Schmitt (1926).

Distribution. Andaman Sea; Indonesia; southern Philippine Islands; Japan; New Caledonia; New Hebrides; Fiji; western Samoa; eastern Australia; 247—828 m.

Heterocarpus woodmasoni Alcock

Heterocarpus Wood-Masoni Alcock, 1901: 108.—Alcock & McArdle, 1901, pl. 51 fig. 2; de Man, 1920: 154, 156—159, pl. 13, figs 36—36c; Calman, 1939: 204.
Heterocarpus woodmasoni.—Kensley, 1972: 50 (in key), fig. 23D; Chace, 1985: 13q.

Material examined. Queensland: AM P25145, east of Fraser Island, 360 m, *Markwell Enterprise,* Jan 1977; 8 specimens.

Diagnosis. Rostrum longer than carapace length, with 7—12 dorsal, and 4—9 ventral spines postrostral crest starting at about anterior quarter of carapace. Carapace with antennal and lateral keels. Abdominal somites 1 and 2 dorsally rounded, somites 3—5 dorsally carinate, somite 6 with paired longitudinal carinae; somite 3 with prominent mid-dorsal hooked spine. Second pair of pereopods markedly unequal, carpus consisting of 20—26 articles in longer, 9—12 articles in shorter.

Remarks. *Heterocarpus woodmasoni* is distinguished from other species of the genus by the presence of a prominent hooked spine dorsally on the third abdominal somite. In the ovigerous females in this series the rostrum is 1.3 to nearly 1.5 times the carapace length and the rostral formula is 8/6 or 8/7.

Distribution. Indian Ocean, Andaman Sea to Indonesia, Philippines, and South China Sea; 291—655 m.

Plesionika Bate, 1888

Plesionika alcocki (Anderson)

Pandalus alcocki Anderson, 1896: 92—93.—Alcock & McArdle, 1901, pl. 52, figs 2, 4; Alcock, 1901: 97—98.
Plesionika alcocki.—Calman, 1939: 197; Chace, 1985: 55.

Material examined. Queensland: AM P35878, P34383, north-east of Point Danger, 28°03′S 154°04′E to 28°01′S 154°04′E, 724 m, demersal prawn trawl, *Kapala* (K78-23-08), 6 Nov 1978; 9 specimens (4 ovig. ♀). New South Wales: AM P25144, north-east of Broken Bay, 33°30′S 152°05′E to 33°27′S 152°07′E, 810 m, demersal prawn trawl, *Kapala* (K76-24-04), 21 Dec 1976; 3 specimens (2 ovig. ♀). AM P35876, east of Broken Bay, 33°32′S 152°06′E to 33°34′S 152°05′E, 808 m, demersal prawn trawl, *Kapala* (K79-20-13), 6 Dec 1979; 5 ovig. ♀. AM P20994, P20998, east of Broken Bay, 33°32′S 152°00′E, 810 m, demersal prawn trawl, *Kapala* (K75-05-05), 19 Aug 1975; 3 specimens. AM 26783, east of Broken Bay, 33°34′S 152°02′E to 33°31′S 152°04′E, 895 m, demersal prawn trawl, *Kapala* (K77-23-07), 6 Dec 1977; 1 specimen. AM P25151, east of Broken Bay, 33°35′S 152°01′E to 33°32′S 152°03′E, 810 m, demersal prawn trawl, *Kapala* (K76-24-03), 20 Dec 1976; 9 specimens (4 ovig. ♀). AM P35877, east of Broken Bay, 33°35′S 152°00′E to 33°33′S 152°02′E, 810 m, demersal prawn trawl, *Kapala* (K77-23-12), 8 Dec 1977; 2 specimens (1 ovig. ♀). AM P19087, south-east of Broken Bay, 33°43′S 151°56′E to 33°40′S 151°59′E, 765 m, demersal prawn trawl, *Kapala* (K72-07-14), 6 Dec 1972; 1 ovig. ♀. AM P19088, south-east of Broken Bay, 32°42′S 151°55′E to 33°40′S 151°57′E, 810 m, demersal prawn trawl, *Kapala* (K72-07-16), 7 Dec 1972; 1 specimen. AM P35872, north-east of Port Jackson, 33°47′S 151°55′E to 33°44′S 151°57′E, 806 m, demersal trawl, *Kapala* (K78-26-16), 7 Dec 1978; 11 specimens (6 ovig. ♀).

Diagnosis. Rostrum immovable, longer than carapace, dorsally unarmed anterior to crest, ventral margin with fewer than 20 fairly widely spaced teeth; rostral crest of 5 sharp teeth, posterior 3 teeth small and movable. Third abdominal somite unarmed posteriorly; fourth abdominal somite without posteroventral denticle on pleuron; fifth abdominal somite with posteroventral denticle on pleuron. Telson with 4 pairs of dorsolateral spines. Eyes well developed, lacking ocellus. Second pair of pereopods subequal, chelate, carpus consisting of 26—32 articles. Third maxilliped with exopod. Pereopods 1—4 with strap-like epipods.

Remarks. The rostrum of the adults in these specimens is just under 1.5 times the carapace length; on the ventral margin there are about eight well spaced teeth, with a further four to five very small teeth near the apex. The second pair of pereopods are subequal in length and exceed the scaphocerite by the length of the chela and the first carpal joint. There are small tufts of setae on the chelae.

In both sexes pereopods three to five have a distinct dactyl which is about one-eighth of the propod length in the fifth pereopod and about one-fifth of the propod length in the third pereopod; there are setae at the bases of the dactyls.

The rostrum of *P. alcocki* is similar to that of *P. martia* (A. Milne Edwards) in being smooth dorsally in front of the rostral crest but *P. alcocki* is distinguished from *P. martia* by having a much shorter rostrum with fewer teeth in the rostral crest and fewer more widely spaced teeth ventrally.

These specimens were collected between 28°S and 34°S in trawls to 900 m depth.

Distribution. Indian Ocean; western Pacific; 500—1412 m.

Plesionika bifurca Alcock & Anderson

Plesionika bifurca Alcock & Anderson, 1894: 155.—Alcock & McArdle, 1901, pl. 51, fig. 6; de Man, 1920: 115, 136—138, pl. 12, figs 31, 31b; Calman, 1939: 199; Chace, 1985: 56, fig. 24.

Pandalus (Plesionika) bifurca.—Alcock, 1901: 98.

Material examined. New South Wales: AM P26809, P26800, north-east of Norah Head, 33°08′S 152°27′E to 33°10′S 152°24′E, 580 m, demersal prawn trawl, *Kapala* (K77-23-09), 7 Dec 1977; 2 specimens. AM P26758, north-east of Norah Head, 33°11′S 152°24′E to 33°09′S 152°25′E, 720 m, demersal prawn trawl, *Kapala* (K77-23-10), 7 Dec 1977; 4 ovig. ♀. AM P25120, east of Broken Bay, 33°35′S 152°01′E to 33°32′S 152°03′E, 810 m, demersal prawn trawl, *Kapala* (K76-24-03), 20 Dec 1976; 1 specimen. AM P19084, south-east to east of Broken Bay, 33°43′S 151°55′E to 33°37′S 152°02′E, 675 m, demersal prawn trawl, *Kapala* (K72-06-04), 19 Oct 1972; 2 specimens. AM P19085, south-east of Broken Bay, 33°44′S 151°55′E to 33°40′S 151°58′E, 720 m, demersal prawn trawl, *Kapala* (K72-07-04), 9 Nov 1972; 1 ovig. ♀. AM P19083, east to north-east of Port Jackson, 33°51′S 151°51′E to 33°45′S 151°55′E, 675 m, demersal prawn trawl, *Kapala* (K72-06-03), 19 Oct 1972; 2 specimens.

Diagnosis. Rostrum immovable, slightly more than half carapace length, rostral crest of 4 teeth behind orbital margin and 2—3 teeth anterior to these on dorsal margin; ventral margin with 3—6 teeth and small subapical tooth. Third abdominal somite dorsally rounded, unarmed posteriorly; fourth abdominal somite without posteroventral denticle; fifth abdominal somite with a posteroventral denticle. Telson with 5 pairs of dorsolateral spines. Eyes well developed, lacking ocellus. Third maxilliped with exopod. Second pair of pereopods chelate, unequal, carpus of shorter with 10—15 articles, of longer with 15—24 articles. Pereopods 1—4 with strap-like epipods.

Remarks. In these specimens the rostrum length is up to two-thirds (0.57—0.67) the carapace length. There are four teeth in the rostral crest behind the orbital margin and two or three anteriorly. On the ventral margin of the rostrum there are usually four or five teeth and one subapical but in two specimens there are only three teeth and in one specimen six teeth as well as the subapical tooth. The telson is about one and one-third times the length of the sixth abdominal segment.

The short rostrum with few widely spaced teeth distinguishes *P. bifurca* from other species of *Plesionika* so far recorded off New South Wales.

These specimens were collected between 33°S and 34°S in trawls to depth of 810 m.

Distribution. Indo-west Pacific to South China Sea and Japan; 245—1412 m.

Plesionika edwardsi (Brandt)

Pandalus Edwardsii Brandt, 1851: 122.

Pandalus longirostris Borradaile, 1899: 413, pl. 37, figs 10, 10a—h.

Plesionika longirostris.—Barnard, 1950: 681—682, fig. 126n; Crosnier, 1976: 234, fig. 4a; Kensley, 1981b: 28 (in list).

Plesionika edwardsii.—Crosnier & Forest, 1973: 202, figs 63b, 64b; Chace, 1985: 62, fig. 26.

Material examined. New South Wales: AM P35890, south-east of Point Danger, 28°17′S 153°53′E to 28°13′S 153°52′E, 198 m, demersal prawn trawl, *Kapala* (K78-17-14), 17 Aug 1978; 8 specimens (6 ovig. ♀). AM P17902, north-east of Norah Head, 33°11′S 152°20′E to 33°14′S 152°16′E, 277 m, demersal prawn trawl, *Kapala* (K71-08-01), 27 Apr 1971; 1 specimen. AM P18101, north-east of Norah Head, 33°11′S 152°20′E to 33°16′S 152°18′E, 274 m, demersal prawn trawl, *Kapala* (K71-14-05), 12 Aug 1971; 15 specimens (12 ovig. ♀). AM P26838, north-east of Batemans Bay, 35°29′S 150°46′E to 35°44′S 150°36′E, 216 m, demersal fish trawl, *Kapala* (K77-11-01/02/03), 2 Aug 1977; 1 specimen. AM P34385, P35889, south-east of Batemans Bay, 35°50′S 150°34′E to 35°46′S 150°36′E, 360 m, demersal fish trawl, *Kapala* (K79-11-04), 7 Aug 1979; 11 specimens (4 ovig. ♀).

Diagnosis. Rostrum immovable, about twice carapace length, with about 4 sharp teeth basally and more than 20 teeth along dorsal margin; ventral margin with more than 30 teeth. Third abdominal somite dorsally rounded, unarmed posteriorly; fourth abdominal somite without posteroventral denticle; fifth abdominal somite with posteroventral denticle. Eyes well developed, ocellus present. Third maxilliped with exopod, last and penultimate articles subequal. Second pair of pereopods chelate, subequal, carpus consisting of 21—25 articles. Pereopods 1—4 with reduced strap-like epipods.

Remarks. In these specimens the rostrum is about twice (1.8—2.3) the carapace length; dorsally the rostrum has four large teeth basally and 21 to 28 anteriorly; ventrally there are 36 to 44 closely-set teeth. The telson is subequal to or slightly less than (1.0—0.9) the length of the sixth abdominal somite.

These specimens were collected between 28°13′S and 35°50′S in trawls to a depth of 360 m.

Distribution. Eastern and western Atlantic, Mediterranean, Gulf of Mexico, Indo-west Pacific; 50—689 m.

Plesionika grahami n. sp.

Figs 20, 21

Type material. New South Wales: HOLOTYPE: AM P35897, north-east of Port Jackson, 33°44′S 151°49′E to 33°42′S 151°50′E, 405 m, trawl, *Kapala,* 28 Sept 1975; 1 ♂, cl 18.4 mm. PARATYPES: AM P35896, east of North Solitary Island, 29°53′S 153°42′E to 29°55′S 153°42′E, 411 m, demersal prawn trawl, *Kapala* (K78-06-06), 26 Apr 1978; 4 specimens (1 ovig. ♀). AM P21583, north-east of Port Jackson, 33°44′S 151°49′E to 33°42′S 151°50′E, 405 m, trawl, *Kapala,* 28 Sept 1975; 2 specimens. AM P26576, north-east of North Solitary Island, 29°52′S 153°43′E to 29°51′S 153°43′E, 500 m, demersal prawn trawl, *Kapala* (K77-13-10), 23 Aug 1977; 2 specimens. AM P21030, north-east of Wollongong, 34°21′S 151°24′E to 34°14′S 151°28′E, 400 m, demersal prawn trawl, *Kapala* (K75-05-02), 8 Aug 1975; 1 specimen. USNM 211400, off Sydney, 33°46′S 151°50′E to 33°42′S 151°53′E, 414 m, demersal prawn trawl, *Kapala* (K80-06-01), 24 May 1980; 7 specimens.

Additional material examined. New South Wales: AM P35904, south-east of Cape Byron, 28°41′S 153°51′E to 28°44′S 153°51′E, 149 m, demersal prawn trawl, *Kapala* (K78-17-21), 18 Aug 1978; 1 specimen. AM P35899, north-east of North Solitary Island, 29°47′S 153°44′E to 29°49′S 153°43′E, 425 m, demersal prawn trawl, *Kapala* (K78-16-07), 2 Aug 1978, 5 specimens. AM P17897, transect from north-east of Newcastle to north-east of Port Jackson, 32°46′S, 152°46′E to 33°44′S, 151°53′E, 540 m, demersal prawn trawl, *Kapala,* Apr 1971; 1 specimen. AM P17996, transect from north-east of Newcastle to east of Port Jackson, 32°46′S 151°48′E to 33°53′S 152°42′E, 191—540 m, demersal prawn trawl, *Kapala,* Apr 1971; 1 specimen. AM P26821, south-east of Newcastle, 32°59′S 152°34′E to 33°02′S 152°42′E, 360 m, demersal prawn trawl, *Kapala* (K77-23-08), 7 Dec 1977; 1 specimen. AM P35898, south-east of Broken Bay, 33°40′S 151°54′E to 33°33′S 151°58′E, 450 m, demersal prawn trawl, *Kapala* (K74-15-25/26) 5 Dec 1974; 1 specimen. AM P35900, south-east of Broken Bay, 33°41′S 151°53′E to 33°39′S 151°56′E, 477 m, prawn trawl, *Kapala* (K80-21-05), 16 Dec 1980; 2 specimens. AM P25210, south-east of Broken Bay, 33°42′S 151°52′E to 33°39′S 151°44′E, 446 m, demersal prawn trawl, *Kapala* (K76-24-01), 20 Dec 1976; 1 specimen. AM P35903, north-east of Port Jackson, 33°46′S 151°49′E to 33°44′S 151°51′E, 425 m, prawn trawl, *Kapala* (K80-21-04), 16 Dec 1980; 2 specimens. AM P19086, east to north-east of Port Jackson, 33°51′S 151°51′E to 33°45′S 151°55′E, 675 m, demersal prawn trawl, *Kapala* (K72-06-03), 19 Oct 1972; 2 specimens. AM P18014, south-east of Wollongong, 34°30′S 151°19′E to 34°38′S 151°13′E, 522 m, demersal prawn trawl, *Kapala* (K71-11-03), 6 July 1971; 1 specimen. AM P24827, north-east of Batemans Bay, 35°28′S 150°50′E to 35°33′S 150°47′E, 594 m, demersal fish trawl, *Kapala* (K76-11-12), 8 July 1976; 4 specimens. AM P35905, north-east of Batemans Bay, 35°34′S 150°44′E to 35°30′S 150°47′E, 400 m, prawn trawl, *Kapala* (K75-12-03), 15 Dec 1975; 1 specimen (bopyrid in right branchial chamber). AM P18015, north-east of Batemans Bay, 35°35′S 150°43′E to 35°35′S 150°50′E, 360 m, demersal prawn trawl, *Kapala* (K71-13-05), 2 Aug 1971; 1 specimen. AM P35901, north-east of Point Danger, 28°06′S 153°58′E to 28°03′S 153°58′E, 404 m, demersal prawn trawl, *Kapala* (K78-09-04), 1 June 1978; 1 ♀. AM P35902, north-east of Point Danger, 27°55′S 154°03′E to 27°57′S 154°03′E, 629 m, demersal prawn trawl, *Kapala* (K78-23-08), 6 Nov 1978; 1 specimen.

Diagnosis. Rostrum over-reaching antennal scale, armed dorsally with 6 or 7 teeth on rostral crest, 3 or 4 posterior to orbital margin, 3 posterior-most teeth articulated; 3 subapical teeth present; armed ventrally with 18—22 teeth. Orbital margin ventrally rounded, posteriorly concave, dorsally sinuous. Abdomen with somite 3 posteriorly unarmed, dorsally compressed but not carinate. Somite 4 and 5, pleura with posteroventral tooth. Somite 6 about 13/5 longer than maximum height, with posteroventral tooth. Telson 12/5 length of somite 6. Eye somewhat compressed; ocellus large, subcircular, narrowly joined to cornea. Stylocerite just over-reaching antennular peduncle article 2. Scaphocerite 4.2X longer than wide; distal tooth not over-reaching apex of blade. Maxilliped 3 with epipod; penultimate article ⅔ length of terminal article. Pereopods 1—4 each with epipod. Legs of pereopod 2 unequal, left long and slender, carpus of about 114 articles, right with 25 articles. Pereopod 3 over-reaching scaphocerite by length of dactyl and distal ⅓ of propodus; dactyl about 1/5 length of propodus, accessory spine almost as long as main terminal spine. Pleopod 3 exopod almost half length of carapace.

Description. Rostrum extending well beyond scaphocerite, distally strongly upturned, about 1.6X carapace length; dorsally with supraorbital crest of 6 or 7 teeth, posterior 2 or 3 of which articulated; remainder of dorsal margin unarmed except for 3 small subterminal teeth; 3—4 teeth posterior to orbital margin; none of teeth barbed; ventral margin armed with 18—22 basally close-set teeth, becoming more widely spaced anteriorly; no postrostral carina or ridge. Orbital margin dorsally sinuous. Antennal spine stronger than pterygostomian spine.

Abdomen with somite 3 posteriorly unarmed, lacking median carina, but somewhat bilaterally compressed, forming ill-defined rounded ridge. Pleuron of somite 3 posteroventrally rounded; those of somites 4 and 5 with posteroventral tooth. Somite 6 about 1.6X length of somite 5, 1.5X longer than wide. Telson about 1.5X length of somite 6, with 4 pairs of dorsolateral spines.

Eye subpyriform, maximum diameter 2/7 length of carapace; ocellus large, subcircular, narrowly connected to cornea.

Antennular stylocerite slender, acute, barely or just over-reaching distal margin of peduncular article 2.

Scaphocerite with lateral margin straight to very slightly convex, $\frac{5}{6}$X length of carapace, about 4.2X longer than wide, distal tooth just falling short of apex of blade.

Mouthparts as illustrated. Maxilliped 3 with epipod, over-reaching scaphocerite by ⅓ of distal article, armed with 1 distal and 4 subterminal spines; penultimate article about ⅔ length of terminal article.

Pereopods 1—4 each with straplike epipod. Pereopod 1 over-reaching scaphocerite by little more than chela, fingers small, movable finger very slightly over-reaching fixed finger. Second pereopods unequal; left elongate, slender, carpus of about 114 articles; right more robust, carpus of 26 articles. Pereopods 3 and 4 over-reaching scaphocerite by dactyl and ⅓ of propodus, with 3 spines on carpus, 7—8 spines on outer and 4 spines on mesial surface of merus. Pereopod 5 over-reaching scaphocerite by slightly more than length of dactyl, armed with 3 spines on outer surface of carpus, 7—9 on outer, and 1—3 on mesial surface of merus, single distal spine on ischium. Endopod of pleopod 1 in male with mesial margin sinuous, small rounded distal lobe bearing hooks. Appendix masculina of pleopod 2 in male longer than appendix interna, with about 16 spines on mesial and distal margin.

Mesial uropodal ramus over-reaching telson, outer ramus slightly longer, with more elongate articulated spine mesial to fixed distolateral tooth.

Remarks. Using the invaluable key to the Indo-Pacific species of *Plesionika* provided by Chace (1985), the present species keys out to *P. rostricrescentis* (Bate), a species known from the Philippines and Indonesia, Japan, New Guinea, and Tonga. However, comparison with the description and with material from the Philippines and Indonesia reveals several major differences, especially in the rostrum and second pereopods (see Table 6).

Etymology. The species is named for Mr Ken Graham, biologist with the Fisheries Division of the NSW Department of Agriculture, who has been responsible for the collection of much of the material described in this report while working on board the FRV *Kapala.*

	P. rostricrescentis	*P. grahami*
rostral crest spines	7—9	6
movable crest spines	5—6	3
ventral rostral teeth	9—15	18—22
carpal articles, pereopod 2		
longer	88	114
shorter	17—21	26
pereopods 3—5		
carpal spines	2	3
meral spines	2 inner, 5 outer	4 inner, 7—8 outer
telson/somite 6 length	1.5	1.2—1.4
Maximum carapace length	18 mm	18—21.8 mm

Table 6. Comparison of *Plesionika rostricrescentis* and *P. grahami.*

Plesionika martia (A. Milne Edwards)

Pandalus martius A. Milne Edwards, 1883: pl.21.
Plesionika martia.—Schmitt, 1926: 377—380; Crosnier,

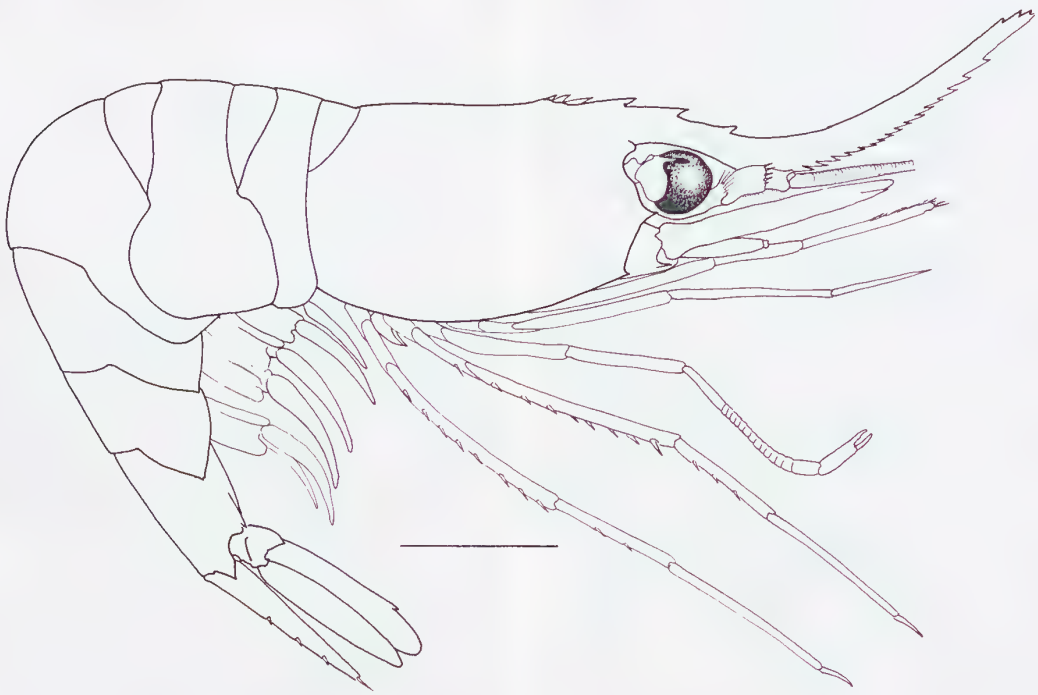

Fig. 20. *Plesionika grahami* n.sp. Lateral view. (Scale = 10 mm).

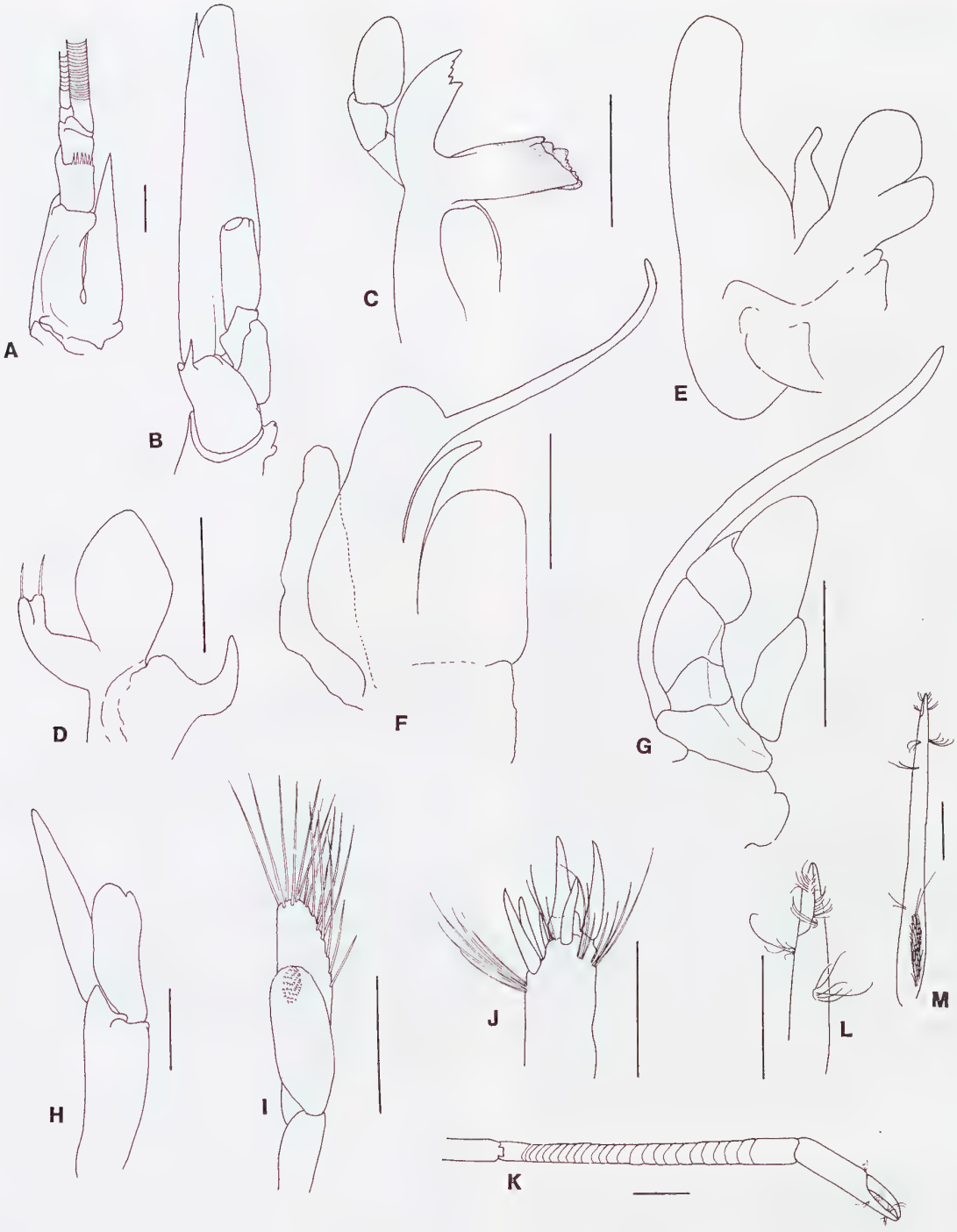

Fig. 21. *Plesionika grahami* n.sp. **A,** antenna 1; **B,** antenna 2; **C,** mandible; **D,** maxilla 1; **E,** maxilla 2; **F,** maxilliped 1; **G,** maxilliped 2; **H,** pleopod 1 ♂; **I,** pleopod 2 ♂, appendix interna and appendix masculina; **J,** apex of dactyl of maxilliped 3; **K,** right pereopod 2; **L,** pereopod 1 chela enlarged; **M,** pereopod 1, dactylus and propodus. (Scales: A-H,K = 2 mm, I-J,L-M = 1 mm).

1970: 235; Kensley, 1972: 50, fig. 23H; 1981b: 28; Crosnier & Forest, 1973: 212—217, figs 63d, 64c, 66.

Material examined. Queensland: AM P35865, north-east of Point Danger, 28°01′S 154°00′E to 27°58′S 154°00′E, 542 m, demersal prawn trawl, *Kapala* (K78-17-10), 17 Aug 1978; 7 specimens (2 ovig. ♀). AM P35866, north-east of Point Danger, 28°03′S 154°04′E to 28°01′S 154°04′E, 724 m, demersal prawn trawl, *Kapala* (K78-23-08), 6 Nov 1978; 3 specimens. New South Wales: AM P35867, east of Yamba, 29°26′S 153°49′E to 29°20′S 153°50′E, 450 m, demersal prawn trawl, *Kapala* (K75-09-08), 12 Oct 1975; 14 specimens (11 ovig. ♀). AM P35868, south-east of Cape Hawke, 32°22′S 152°51′E to 32°17′S 153°01′E, 463 m, demersal prawn trawl, *Kapala* (K75-08-03) 12 Oct 1975; 13 specimens (6 ovig. ♀). AM P17899, transect from north-east of Newcastle to east of Port Jackson, 32°46′S 151°48′E to 33°53′S 152°42′E, 191—540 m, demersal prawn trawl, *Kapala,* Apr 1971; 4 specimens. AM P19640, transect from east of Newcastle to north-east of Port Jackson, 33°00′S 152°31′E to 33°44′S 151°50′E, 355 m, demersal prawn trawl, *Kapala,* July 1972; 2 specimens (ovig. ♀). AM P17898, north-east of Norah Head, 33°11′S 152°20′E to 33°14′S 152°16′E, 277 m, demersal prawn trawl, *Kapala* (K71-08-01), 27 Apr 1971; 2 ovig. ♀. AM P35869, east of Broken Bay, 33°35′S 152°00′E to 33°33′S 152°02′E, 810 m, demersal prawn trawl, *Kapala* (K77-23-12), 8 Dec 1977; 1 specimen. AM P25209, south-east of Broken Bay, 33°42′S 151°52′E to 33°33′S 151°54′E, 446 m, demersal prawn trawl, *Kapala* (K76?24-01), 20 Dec 1976; 11 specimens (5 ovig. ♀). AM P18992, south-east of Broken Bay, 33°42′S 151°55′E to 33°40′S 151°57′E, 810 m, demersal prawn trawl, *Kapala* (K72-07-16), 7 Dec 1972; 8 specimens. AM P18983, south-east of Broken Bay, 33°43′S 151°56′E to 33°40′S 151°59′E, 765 m, demersal prawn trawl, *Kapala* (K72-07-14), 6 Dec 1972; 1 specimen. AM P21586, north-east of Port Jackson, 33°44′S 151°49′E to 33°42′S 151°50′E, 405 m, trawl, *Kapala,* 28 Sept 1975; 4 specimens. AM P18978, south-east of Broken Bay, 33°44′S 151°55′E to 33°40′S 151°58′E, 720 m, demersal prawn trawl, *Kapala* (K72-07-04), 9 Nov 1972; 1 specimen. AM P21041, P21049, north-east of Wollongong, 34°16′S 151°26′E to 34°22′S 151°23′E, 356 m, prawn trawl, *Kapala* (K75-05-01), 8 Aug 1975; 2 ovig. ♀. AM P21046, north-east of Wollongong, 34°21′S 151°24′E to 34°14′S 151°28′E, 400 m, demersal prawn trawl, *Kapala* (K75-05-02), 8 Aug 1975; 3 specimens (2 ovig. ♀). AM P35870, north-east of Wollongong, 34°24′S 151°25′E to 34°23′S 151°25′E, 738 m, prawn trawl, *Kapala* (K76-23-01), 13 Dec 1976; 1 specimen. AM P34386, south-east of Broken Bay, 33°43′S 151°54′E to 33°39′S 151°55′E, 531—423 m, prawn trawl, *Kapala* (K83-14-07), 27 Oct 1983; 3 ♂, 2 ovig. ♀.

Diagnosis. Rostrum immovable, about twice carapace length, rostral crest of 7—9 sharp teeth, dorsal margin anterior to crest smooth, ventral margin with 37 or more teeth. Third abdominal somite dorsally rounded, unarmed posteriorly; fourth abdominal somite without posteroventral denticle; fifth abdominal somite posteroventrally sharp, usually with denticle. Telson with 4 pairs of dorsolateral spines. Eyes well developed, ocellus present. Third maxilliped with exopod. Pereopods 1—4 with strap-like epipod. Second pair of pereopods chelate, subequal, carpus consisting of 18—36 articles.

Remarks. In these specimens the rostrum is about twice the carapace length in the adults and up to 2.5 times the carapace length in smaller (cl 13—16 mm.) specimens. Most of the specimens have seven or eight spines dorsally on the rostrum but the range over all the specimens is from six to ten spines. The number of spines ventrally on the rostrum ranges from 37 to 60. The dactyl of the third pereopod is slightly less than a third the length of the propod. The length of the sixth abdominal segment is about twice the maximum height.

The rostrum of this species is, like that of *P. alcocki,* smooth on the dorsal margin ahead of the rostral crest but *P. martia* is distinguished from *P. alcocki* by its longer rostrum, more teeth in the rostral crest and more teeth more closely spaced on the ventral margin of the rostrum.

These specimens were collected between 28°S and 34°25′S in trawls to a depth of 810 m.

Distribution. Western and eastern Atlantic and throughout the Indo-West Pacific; 277—900 m.

Plesionika reflexa Chace

Plesionika reflexa Chace, 1985: 108, fig. 49.

Material examined. Queensland: AM P35875, north-east of Point Danger, 27°55′S 154°03′E to 27°57′S 154°03′E, 629 m, demersal prawn trawl, *Kapala* (K78-23-09), 6 Nov 1978; 2 specimens. AM P34384, north-east of Point Danger, 28°01′S 154°00′E to 27°58′S 154°00′E, 542 m, demersal prawn trawl, *Kapala* (K78-17-10), 17 Aug 1978; 3 specimens (1 ovig. ♀). New South Wales: AM P35873, transect from north-east of Newcastle to east of Port Jackson, 32°46′S 151°48′E to 33°53′S 152°42′E, 191—540 m, demersal prawn trawl, *Kapala,* April 1971; 1 specimen. AM P21587, north-east of Port Jackson, 33°44′S 151°49′E to 33°42′S 151°50′E, 405 m, trawl, *Kapala* (no stn), 28 Sept 1975; 1 specimen. AM P35874, north-east of Port Jackson, 33°46′S 151°49′E to 33°44′S 151°51′E, 425 m, demersal prawn trawl, *Kapala* (K80-21-04), 16 Dec 1980; 3 specimens. AM P21042, north-east of Wollongong, 34°16′S 151°26′E to 34°22′S 151°23′E, 356 m, demersal prawn trawl, *Kapala* (K75-05-01), 8 Aug 1975; 1 specimen.

Diagnosis. Rostrum immovable, posteriorly curved ventrally, anteriorly curved dorsally, about twice carapace length or longer, 5 or 6 sharp teeth proximally, remainder of dorsal margin smooth except for subapical spine, ventral margin with more than 30 teeth. Third abdominal somite with posteromedian spine slightly recurved dorsally. Eyes well developed. Maxilliped 3 with exopod. Second pair of pereopods subequal, chelate, carpus consisting of more than 3 segments. Pereopod 3 with dactyl between 0.29 and 0.4 length of propodus. Pereopods 1—4 with strap-like epipods.

Remarks. These specimens agree in general with the specimens figured by Suseeland & Mahomed (1968), and Crosnier & Forest (1973), as *P. ensis* (A.

Milne Edwards), but differ slightly in some of the characters. In the largest specimen (cl. 21.7mm) the rostrum is less than twice (1.8) carapace length. In all the other specimens in which the rostrum is complete or nearly so, the rostrum is more than twice (2.2—2.5) the carapace length. The denticulation on the ventral margin of the rostrum usually starts behind the anterior dorsal tooth opposite the first article of the antennal peduncle. The first and second pereopods are subequal in length and reach to about 2—4 mm behind the apex of the scaphocerite. The third pereopod is the longest, and reaches to at least the apex of the scaphocerite or more usually exceeds it by the dactyl. The dactyl of the third pereopod is about one-third the length of the propod. The length of the sixth abdominal somite is at least 2.5 times (2.5—2.9) its proximal height, and more than twice (2.2—2.5) the length of the fifth somite. The telson is about three-fourths (0.75—0.8) as long as the sixth somite. In two critical characters, the length of the dactyl of pereopod 3 compared with the propodus, and the slight recurving of the mid-dorsal spine of abdominal somite 3, the present material agrees with the description of *P. reflexa* Chace.

These specimens were collected between 27°55′S and 34°22′S in trawls down to 629 m.

Distribution. South China Sea; Indonesia; Philippines; 191—629 m.

Plesionika spinipes Bate

Plesionika spinipes Bate, 1888: 646—648, pl. 113, fig. 2.—Chace, 1985: 46 (in key).
Parapandalus spinipes.—de Man, 1920: 142—146, pls 12, 13, figs 33, 33e; Calman, 1939: 201—202; Crosnier, 1970: 236 (in discussion).

Material examined. New South Wales: AM P35888, north-east of North Solitary Island, 29°47′S 153°41′E to 29°49′S 153°40′E, 234 m, demersal prawn trawl, *Kapala* (K78-05-07), 19 Apr 1978; 1 ovig. ♀. AM P26839, north-east and east of Batemans Bay, 35°29′S 150°46′E to 35°44′S 150°36′E, 216 m, demersal fish trawl, *Kapala* (K77-11-01/02/03), 2 Aug 1977; 1 specimen. Queensland: AM P35871, north-east of Point Danger, 28°02′S 153°57′E to 28°05′S 153°57′E, 360 m, demersal fish trawl, *Kapala* (K78-09-03), 1 June 1978; 20 specimens (13 ovig. ♀).

Diagnosis. Rostrum about twice carapace length, with fewer than 50 close-set dorsal teeth, and 22—31 more widely spaced ventral teeth. Eyes well developed, ocellus present. Pereopods 1—4 lacking epipods. Pleura of abdominal somites 4 and 5 each with posteroventral denticle.

Remarks. These specimens agree with that figured by de Man (1920) as *Parapandalus spinipes* (Bate). The rostrum is complete in only a few specimens; in these it is nearly twice (1.7—2.0) the carapace length. The rostral teeth are similarly spaced on the dorsal and ventral margins in the distal two-thirds, while basally the dorsal spines are more closely spaced. Both the fourth and fifth abdominal somites have a posteroventral denticle as in the figure of *P. spinipes* provided by de Man (1920); in *P. serratifrons* (Borradaile) the fourth abdominal somite lacks a denticle.

Crosnier (1976) gives a table, based principally on literature, for distinguishing *P. spinipes, P. serratifrons* and *P. narval.* For our specimens the measurements used are: rostral formula: 41—51/25—35; minimum width of abdominal somite 6/length of this somite: 0.37—0.4; maximum height of abdominal somite 6/length of this somite: 0.56—0.6; length of telson/length of abdominal somite 6: 1.15—1.2; length of dactyl of pereopod 5/basal width of this dactyl: 4.

There is agreement in the first three sets of figures, with those given by Crosnier (1976), but the telson is less than 1.5 times the length of abdominal somite 6, and the pereopodal dactyls are not as slender. Unfortunately, in many specimens the telson and rostrum are damaged and pereopodal dactyls are detached; we therefore provide details of the relative lengths of maxilliped 3 and pereopods 1 and 2 of our specimens. These agree with de Man's description and figures for *P. spinipes;* these appendages are longer in relation to the scaphocerite in *P. serratifrons.* In ovigerous females (cl 19 mm) maxilliped 3 exceeds the scaphocerite only by the terminal article; the penultimate article is about 1.75 times the length of the terminal article, while the exopod reaches about halfway along the antepenultimate article. Pereopod 1 exceeds the scaphocerite by the terminal article and about one-third of the carpus; it exceeds maxilliped 3 by about half the terminal article. Pereopod 2 exceeds the scaphocerite by the chela and the large terminal article of the carpus. The carpus has 21—23 articles. In a smaller specimen (cl 12.5 mm) the relative lengths are slightly different; maxilliped 3 exceeds the scaphocerite by slightly more than the terminal article, and the exopod does not quite reach halfway along the antepenultimate article.

Pereopod 1 exceeds the scaphocerite by the dactyl and just less than half the carpus, and exceeds maxilliped 3 by three-fourths of the terminal article. Pereopod 2 exceeds the scaphocerite by the chela and distal three articles of the carpus.

Distribution. Indo-West Pacific.

Stylopandalus Coutiere, 1905

Stylopandalus richardi (Coutiere)

Pandalus (Stylopandalus) Richardi Coutiere, 1905: 1113.
Parapandalus richardi.—Crosnier & Forest, 1973: 224—225, fig. 69b; Kensley, 1981a: 59, 1981b: 28.
Stylopandalus richardi.—Chace 1985: 136, fig. 62.

Material examined. New South Wales: AM P35879, north-east of Norah Head, 33°05′S 153°05′E to 33°13′S 153°05′E, 630 m, midwater trawl, *Kapala* (K79-19-03), 28 Nov 1979; 1 ovig. ♀. AM P35880, east to north-east of

Norah Head, 33°20′S 153°04′E to 33°12′S 153°13′E, 630 m, midwater trawl, *Kapala* (K79-19-05), 28 Nov 1979; 5 specimens (4 ovig. ♀). AM P35881, south-east of Norah Head, 33°20′S 152°32′E to 33°24′S 152°31′E, 360 m, midwater trawl, *Kapala* (K77-24-09), 14 Dec 1977; 1 ovig. ♀. AM P35882, north-east to east of Broken Bay, 33°28′S 152°34′E to 33°36′S 152°35′E, 630 m midwater trawl, *Kapala* (K77-24-10), 14 Dec 1977; 2 ovig. ♀. AM P35883, north-east of Broken Bay, 33°31′S 152°20′E to 33°28′S 152°22′E, 569 m, midwater trawl, *Kapala* (K77-24-02), 12 Dec 1977; 1 ovig. ♀. AM P35884, east of Broken Bay, 33°33′S 152°18′E to 33°31′S 152°18′E, 216 m, midwater trawl, *Kapala* (K77-24-01), 12 Dec 1977; 2 specimens (1 ovig. ♀). AM P35885, P34387, north-east of Wollongong, 34°10′S 151°59′E to 34°09′S 152°05′E, 0—about 60 m, midwater trawl, *Kapala* (JP71-3), 24 Mar 1971; 19 specimens (4 ovig. ♀). AM P26558, north-east of Wollongong, 34°10′S 152°04′E to 34°12′S 152°02′E, 540 m, midwater trawl, *Kapala* (K77-18-01), 26 Oct 1977; 4 specimens (1 ovig. ♀). AM P35886, north-east to east of Wollongong, 34°20′S 151°56′E to 34°25′S 151°54′E, 630 m, midwater trawl, *Kapala* (K77-24-12), 14 Dec 1977; 2 specimens (1 ovig. ♀). AM P26602, north-east of Cape Howe, 37°24′S 150°30′E to 37°28′S 150°33′E, 540 m, midwater trawl, *Kapala* (K77-19-03), 1 Nov 1977; 2 specimens (1 ovig. ♀). AM P35887, north-east of Wollongong, 34°10′S 152°04′E to 34°12′S 152°02′E, 540 m, midwater trawl, *Kapala* (K77-18-01), 26 Oct 1977; 1 specimen.

Diagnosis. Rostrum immovable, 2.5—3X carapace length, both dorsal and ventral margins with rather well spaced teeth along their length, 2 larger teeth at base of the rostrum. Carapace with no distinct longitudinal carina except behind rostral crest. Third abdominal segments armed posteriorly with minute medial spine; both fourth and fifth abdominal segments without a posteroventral denticle; length of sixth abdominal segment about 3X its maximum height. Eyes well developed. Third maxilliped with exopod. Second pair of pereopods chelate, subequal, carpus consisting of 7—13 articles. Pereopods 1—4 without epipods.

Distribution. Indo-west Pacific, Philippines, north and south Atlantic; surface to 3600 m.

Family PHYSETOCARIDIDAE

Physetocaris Chace, 1940

Physetocaris microphthalma Chace

Physetocaris microphthalma Chace, 1940: 196, figs 62,63.—Holthuis, 1955: 128, fig. 93; Crosnier & Forest, 1973: 228, fig. 72.

Material examined. New South Wales: AM P33107, north-east of Broken Bay, 33°31′S 152°20′E to 33°38′S 152°22′E, 569 m, midwater trawl, *Kapala* (K77-24-02), 12 Dec 1977; 1 specimen.

Diagnosis. Integument thin and fragile. Rostrum a broadly triangular inflated prolongation of carapace, latter inflated, with 2 lateral carinae. Abdomen lacking dorsal carinae or spines. Telson dorsally deeply sulcate, apically broadly truncate. Eyes reduced, set on outer surface of stalk. Mandible lacking palp and incisor process. First pereopods simple. Second pereopods chelate, carpus of 4 articles. Exopods absent from third maxilliped and all pereopods.

Distribution. Eastern and western Atlantic, north-west Pacific; surface to 1600 m.

Family GLYPHOCRANGONIDAE

Glyphocrangon A. Milne Edwards, 1881

Glyphocrangon assimilis de Man

Glyphocrangon assimilis de Man, 1918: 294; 1920: 217, 227—230, pl. 19, figs 57—57h.—Calman, 1939: 217; Chace, 1984: 9.

Material examined. Queensland: AM P33151, north-east of Danger Point, 28°03′S 154°04′E to 28°01′S 154°04′E, 720 m, demersal prawn trawl, *Kapala* (K78-23-08), 6 Nov 1978; 2 specimens. New South Wales: AM P33152, east of Broken Bay, 33°34′S 152°04′E to 33°31′S 152°06′E, 720 m, demersal prawn trawl, *Kapala* (K79-20-04), 4 Dec 1979; 2 specimens (1 ovig. ♀). AM P26823, east of Broken Bay, 33°35′S 152°00′E to 33°33′S 152°02′E, 810 m, demersal prawn trawl, *Kapala* (K77-23-12), 8 Dec 1977; 1 ovig. ♀.

Diagnosis. Integument not pubescent. Rostrum dorsoventrally compressed, shorter than carapace, with 2 pairs of lateral spines. Carapace with 4 prominent lateral carinae; anterior antennal carina present, with anterior spine behind and slightly ventral to antennal spine, carina extending only halfway to lateral groove, with 2 tubercles in line behind it; anterior lateral carina with small anterior spine well posterior to orbital margin.

Remarks. These specimens agree well with the description and figures given by de Man (1920).

The length of the rostrum is about four-fifths (0.77—0.81) of the carapace length in the largest male and the two females (cl 16.5—18.5 mm), while in the two smaller males (cl 13, 15 mm) it is subequal (0.96—1.0).

The submedian carinae are made up of distinct tubercles. The anterior intermediate carina consists of four to five distinct tubercles of which at least the two most anterior are acute. The posterior intermediate carina is variable, sometimes consisting of four to five tubercles, in other cases of three broad tubercles, or a ridge with two notches or even an unnotched ridge. None of the other carapace carinae are tuberculate. The anterior antennal carina has an anterior spine behind and slightly below the antennal spine and the carina extends backwards only halfway to the lateral groove, with two to three small tubercles in line between the end of the carina and the groove. This character distinguishes this species from *G. dentatus* Barnard and *G. gilesii* Wood-Mason, in both of which the carina extends all the way to the lateral

groove. The anterior lateral carina has an anterior spine and the carina extends back to the lateral groove. Neither the posterior antennal nor the posterior lateral carina has an anterior spine.

The carapace surface between the submedian carinae is smooth and between the other carinae there are only very small tubercles which are near the posterior border in the males, and scattered over the posterior two-thirds in the females.

The antennal spine is longer than the branchiostegal spine. There are dorsal carinae present on all the abdominal segments.

These specimens were collected from 28°S to 33°40′S and at depths between 720 and 810 metres. This species has not been recorded previously from Australia.

Colour. The colour in life is white with the submedian, intermediate, and abdominal carinae orange red. The rostrum, antennal, and branchiostegal spines are coloured pale orange only at the tips.

Distribution. Zanzibar, Bali Sea, eastern Australia; 538—810 m.

Glyphocrangon holthuisi n. sp.

Figs 22, 25C

Type material. New South Wales: HOLOTYPE: AM P35906, south-east of Cape Byron, 28°41′S 153°52′E to 28°44′S 153°51′E, 153 m, prawn trawl, *Kapala* (K78-17-21), 18 Aug 1978; 1 ovig. ♀, cl 25.1 mm. PARATYPES: AM P33157, south-east of Cape Byron, 28°41′S 153°52′E to 28°44′S 153°51′E, 153 m, prawn trawl, *Kapala* (K78-17-21), 18 Aug 1978; 16 ovig. ♀. Queensland: PARATYPES: USNM 211397, north-east of Danger Point, 28°01′S 154°00′E to 27°58′S 154°00′E, 540 m, prawn trawl, *Kapala* (K78-17-10), 17 Aug 1978; 5 ♂, cl 19.2—22.0 mm, 5 ovig. ♀, 21.2—24.9 mm.

Additional material examined. AM P33153, north-east of Danger Point, 27°55′S 154°03′E to 27°57′S 154°03′E, 540 m, prawn trawl, *Kapala* (K78-23-09), 6 Nov 1978; 8 ♂, cl 15.2—21.8 mm, 17 ovig. ♀, cl 18.5?-25.2 mm, 5 ♀, cl 14.0—18.4 mm. AM P33154, north-east of Danger Point, 28°01′S 154°00′E to 27°58′S 154°00′E, 540 m, prawn trawl, *Kapala* (K78-17-10) 17 Aug 1978; 34 ovig. ♀, 64 ♂. AM P33155, north-east of Danger Point, 28°02′S 153°59′E to 27°59′S 153°59′E, 540 m, prawn trawl, *Kapala* (K78-09-05), 2 June 1978; 63 specimens (16 ovig. ♀). AM P33156, north-east of Danger Point, 28°03′S 154°04′E to 28°01′S 154°04′E, 720 m, prawn trawl, *Kapala* (K78-23-08), 6 Nov 1978; 11 specimens.

Diagnosis. Integument firm, finely tomentose. Rostrum anteroventrally tricarinate, with 2 pairs of lateral spines and faint mid-dorsal ridge. Posterior first (submedian carina) of 3 or 4 discrete tubercles. Anterior second (intermediate) carina with anterior tubercle acute; posterior second (intermediate) carina tuberculate. Anterior third (antennal) carina absent; posterior third (antennal) carina anteriorly right-angled to rarely acute, usually consisting of 2 elongate and 1 short posterior tubercles. Anterior fourth (lateral) carina expanded into large ventically compressed undivided lamina, apically acute, obliquely directed; posterior fourth (lateral) carina divided into 2 elongate anterior, and 2 or 3 smaller apically acute posterior tubercles. Branchial region with tubercles between carinae. Smooth antennal spine very faintly mesially curved, more than half length of branchiostegal spine. All abdominal somites with mid-dorsal carina, notched on somite 6. Scaphocerite lacking marginal tooth. Maximum carapace length 25.2 mm (ovigerous female).

Description. Integument finely tomentose. Rostrum in adults about two-thirds (0.59—0.71) carapace length, armed with 2 pairs of lateral teeth, anterior pair at about proximal two-fifths; faint mid-dorsal ridge present with transverse septa sometimes present anteriorly, but often indistinct; anteroventrally tricarinate. Submedian (1st) carina composed of elongate laterally compressed tubercles, acute or subacute at the anterodorsal angle, anterior carina with 6 tubercles, posterior carina with 3—4 tubercles. Anterior intermediate (2nd) carina usually with all 4 tubercles dentiform (as in submedian carina), posterior carina with 4 (sometimes 3 or 5) tubercles, usually not dentiform. Anterior antennal (3rd) carina absent. Posterior antennal (3rd) carina usually unarmed anteriorly, rarely with small tooth, carina divided by 2 or 3 notches. Anterior lateral (4th) carina not continuous with branchiostegal spine, expanded into large, vertically compressed, undivided lamina, apically acute, directed forward beyond level of the posterior margin of the orbit. In adults, width across tips of these spines less than (0.93—0.96), or rarely equal to, carapace length. Posterior lateral (4th) carina usually with 3 notches but varying from 2—4, and rarely with only 1 notch or entire; usually with small anterior spine but quite often with only a sharp angle.

Tubercles between carapace carinae small, usually acute, rows often irregular. Usually 3 rows of tubercles between third and fourth carinae, tubercles of central row largest, with row of small tubercles above and below. Area of carapace immediately posterior to eye usually with 3—5 tubercles (occasionally with 6—7 or with only 1—2).

Antennal spine curved mesially, smooth, about three-fourths (0.74—0.91) as long as the branchiostegal spine. Tip of branchiostegal spine not exceeding propodus of pereopod 1, nor reaching distal end of penultimate segment of maxilliped 3.

Abdomen with median dorsal carinae on all somites, somite 1 with distinct anterior tubercles in addition to row of narrow tubercles along posterior margin, lateral-dorsal carina on somite 1 with anterior height equal to about half basal length of carina. Somite 5 with 2 marginal spines on pleuron. Somite 6 with 1 posterior marginal spine on pleuron, width of somite across these spines only slightly greater than (1.1—1.25) anterior width of somite 6.

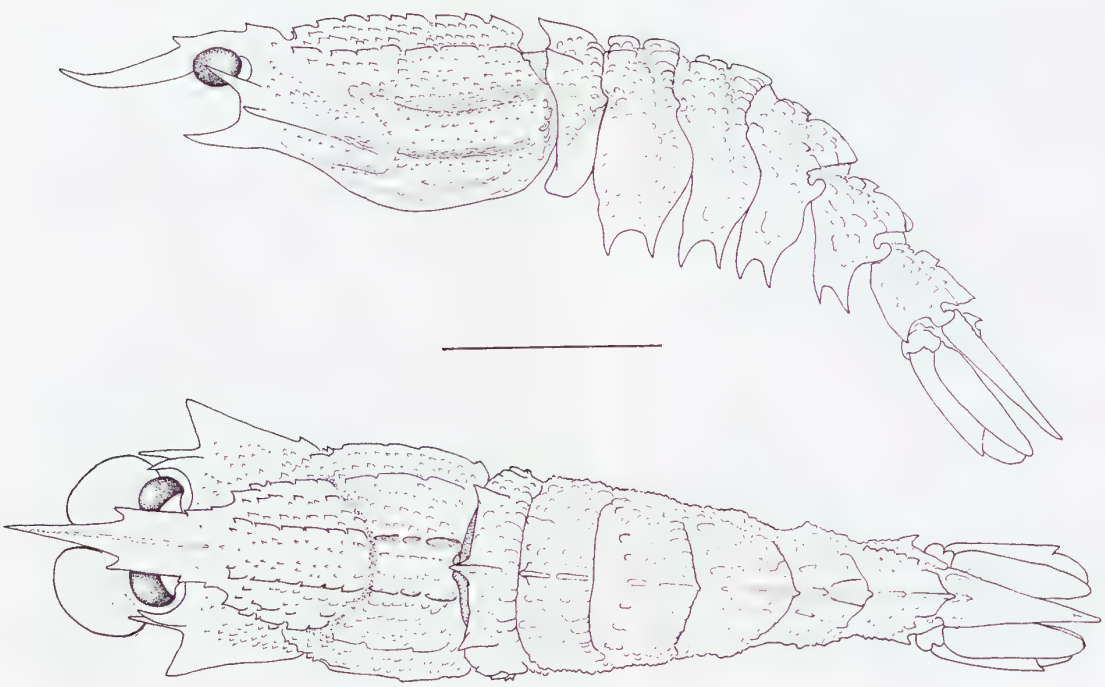

Fig. 22. *Glyphocrangon holthuisi* n.sp. Lateral and dorsal view. (Scale = 10 mm).

Telson with about 1/5 of its length extending beyond uropods.

Antennal scale about one and three-fourths (1.68—1.81) times as long as broad, nearly twice as long as broad in small specimens (cl 15 mm). Maxilliped 3 extending as far as, or very slightly past, end of antennal peduncle. Pereopod 2 shorter on left side (19—20 carpal articles) than on right side (29 carpal articles). Left pereopod 2 on just reaching to end of antennal scale; on right, exceeding antennal scale by chela and about 8 carpal articles. Pereopod 3 reaching as far forward as pereopod 2 on left side. Pereopod 4 reaching to about end of propod of pereopod 3. Pereopod 5 reaching about ⅔ along propod of pereopod 4. Pereopods 3 to 5 with propod about 1¼ to 1⅓ as long as carpus; dactyl about ⅓ to 2/5 length of propod.

Etymology. The species is named for Dr L. B. Holthuis, of the Rijksmuseum van Natuurlijke Historie, Leiden, in recognition not only of his valuable work on the genus *Glyphocrangon,* but also of his incomparable contributions to the knowledge of crustaceans.

Remarks. See Remarks section of *G. novacastellum.*

Glyphocrangon lowryi n. sp.

Figs 23, 25D

Type material. Queensland: HOLOTYPE: AM P33158, north-east of Danger Point, 28°03′S 154°04′E to 28°01′S 154°04′E, 720 m, prawn trawl, *Kapala* (K78-23-08), 6 Nov 1978; 1 ovig. ♀, cl 31.5 mm.

Diagnosis. Integument firm, lacking tomentum. Rostrum with 2 pairs lateral spines, with rounded mid-dorsal ridge, anteriorly with faint transverse septa, anteroventrally bicarinate. Anterior third (antennal) carina absent, posterior third carina with acute flattened flared spine. Anterior fourth (lateral) carina anteriorly expanded into large vertically compressed undivided apically acute lamina; carapace width across these tips subequal to carapace length. Tubercles of submedian carina laterally compressed; tubercles between carapace carinae high, laterally compressed.

Description. Integument naked. Rostrum in adult female greater than half carapace length (tip broken, estimated between 0.5 and 0.6), armed with 2 pairs of lateral teeth, anterior pair at about proximal third; medial ridge present, tuberculate proximally with 2 pairs of submedial tubercles near base;

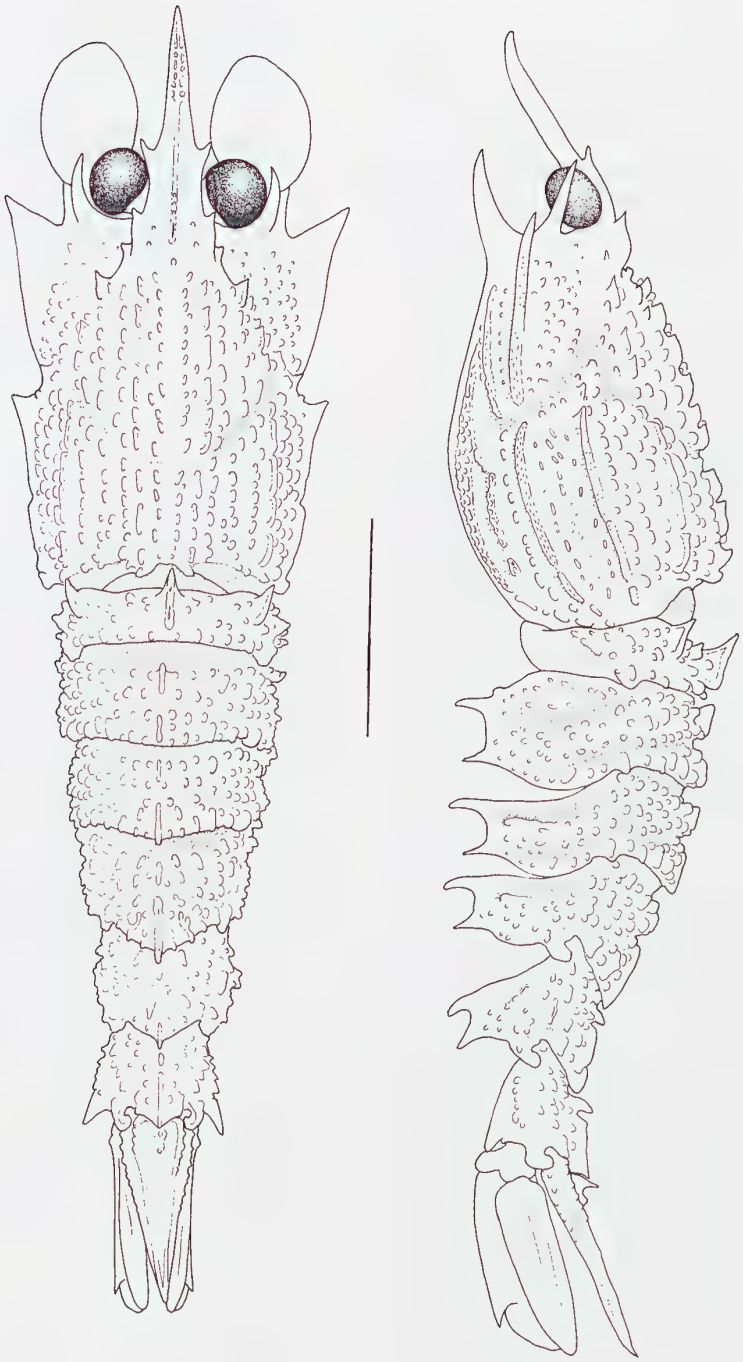

Fig. 23. *Glyphocrangon lowryi* n.sp. Lateral and dorsal view. (Scale = 10 mm).

indistinct transverse septa anteriorly; 2 lateral, but no anteromedial ridge ventrally on rostrum. Submedian (1st) carina composed of elongate laterally-compressed tubercles, only a few anterior tubercles subacute anteriorly, remainder blunt, anterior carina with 6 tubercles; posterior carina with 4 or 5 tubercles. Anterior intermediate (2nd) carina of 4 tubercles, some hardly distinguishable from large tubercles between the carinae, 2 anterior tubercles anterodorsally; posterior carina of 4 blunt elongate tubercles. Anterior antennal (3rd) carina absent; posterior antennal carina with spine anteriorly, carina with 2 notches, one at about midlength, one near posterior extremity. Carapace width across spines of posterior pair about nine-tenths (0.89) of carapace length (0.92 cl in immature specimens, cl 17.8 mm). Anterior lateral (4th) carina not continuous with branchiostegal spine, expanded into large compressed undivided apically acute lamina, directed forward beyond level of posterior margin of orbit. In ovigerous female, width across these spines slightly less (0.97) than carapace length. Posterior lateral carina entire except for one notch at about posterior sixth, anteriorly unarmed and curving slightly dorsally. Tubercles between carinae high, laterally compressed, not as elongate as carinae tubercles, often in regular rows. About 5 tubercles on carapace immediately behind eye, high tubercle lateral to posterior lateral rostral spine. Antennal spine weakly curved mesially, smooth, about ¾ length of branchiostegal spine. Tip of branchiostegal spine just exceeding propod of pereopod 1, reaching distal margin of penultimate segment of maxilliped 3.

Abdomen with median dorsal carina on all somites, somite 1 with prominent anterior tubercles in addition to row of tubercles along posterior margin, lateral dorsal carina on somite 1 with anterior height equal to basal length of carina. Somite 5 with 2 marginal spines on pleuron. Somite 6 with 1 posterior marginal spine on pleuron, width across these spines more than one and one-third (1.42) times anterior width of somite 6 (1.5X in immature specimen, cl 14.2 mm). Telson with less than 1/5 of its length extending beyond apex of uropods; submedial carina tuberculate on proximal quarter, marginal carina tuberculate on proximal half.

Antennal scale about one and one-half (1.6) times as long as broad, extending about 1/5 of its length beyond antennal peduncle. Pereopod 2 shorter on left (20 carpal articles) than on right side (29 carpal articles). On left side, pereopod 2 exceeding antennal scale by chela and 1 carpal article, on right side exceeding antennal scale by chela and about 10 carpal articles. Pereopod 3 exceeding antennal scale by length of dactyl. Pereopod 4 reaching about halfway along dactyl of pereopod 3. Pereopod 5 reaching to base of dactyl of pereopod 4. Propod of pereopods 3 and 4 more than one and one-third (1.4) times as long as carpus; on perepod 5, 1⅓X as long. Dactyl of pereopod 3 about one-third (0.3) length of propod; dactyl of pereopods 4 and 5 more than one-third (0.41 and 0.37 respectively) length of propod.

Colour. The preserved ovigerous female has orange tips on the apical and lateral spines of the rostrum, on the antennal and branchiostegal spines, and on the tip of the anterior lateral carina. Also the last segment of maxilliped 3, and the propod and dactyl of pereopod 1 are orange. On abdominal somites 1—4 the tips of the carinae and spines on the pleura are orange, as is the tip of the telson.

Etymology. The species is named for Dr James K. Lowry, head of the Crustacean Section of the Australian Museum, in thanks for his hospitality to, and many stimulating discussions with, the first author.

Remarks. See Remarks section at end of *G. novacastellum.*

Glyphocrangon novacastellum n. sp.

Figs 24, 25E

Type material. New South Wales: HOLOTYPE: AM P26766, south-east of Newcastle, 33°08′S 152°27′E to 33°09′S 152°25′E, 720 m, demersal trawl, *Kapala* (K77-23-10), 7 Dec 1977; 1 ovig. ♀, cl 25.0 mm. PARATYPES: AM P20995, P20996, east of Broken Bay, 33°32′S 152°00′E to 33°38′S 152°04′E, 823 m, demersal trawl, *Kapala* (K75-05-05), 6 Dec 1979; 2 ♂, cl 15.9—16.0 mm, 10 ovig. ♀, 21.1—24.6 mm, 1 ♀, cl 15.9 mm. AM P33160, east of Broken Bay, 33°32′S 152°06′E to 33°34′S 152°05′E, 810 m, demersal prawn trawl, *Kapala* (K79-20-13), 6 Dec 1979; 1 ovig. ♀, cl 24.3 mm. AM P19096, east of Long Reef, 33°43′S 151°55′E to 33°37′S 152°02′E, 675 m, bottom trawl, *Kapala* (K72-06-04), 19 Oct 1972; 1 ovig. ♀, cl 20.7 mm. USNM 211399, off Shoalhaven Bight, 34°55′S 151°13′E to 34°53′S 151°14′E, 810 m, demersal trawl, *Kapala* (78-27-05), 12 Dec 1978; 1 ♂, cl 18.3 mm, 2 ovig. ♀, cl 20.1 mm, 2 ♀, cl 16.2—18.3 mm. USNM 211398, south-east of Newcastle, 33°08′S 152°27′E to 33°10′S 152°24′E, 576 m, demersal trawl, *Kapala* (K77-23-09), 7 Dec 1977; 1 ovig. ♀, cl 25.0 mm.

Additional material examined. New South Wales: AM P33161, east of Broken Bay, 33°34′S 152°04′E to 33°31′S 152°06′E, 720 m, prawn trawl, *Kapala* (K79-20-04), 4 Dec 1979; 1 ♀, cl 16.0 mm. AM P26822, east of Broken Bay, 33°34′S 152°02′E to 33°31′S 152°04′E, 891 m, demersal trawl, *Kapala* (K77-23-07), 6 Dec 1977; 1 specimen. AM P19099, east of Sydney, 33°42′S 152°50′E to 33°48′S 152°54′E, 765 m, bottom trawl, *Kapala* (K72-07-15), 7 Dec 1972; 1 ♂, cl 22.6 mm.

Diagnosis. Body integument very firm, covered with fine tomentum. Rostrum dorsally with septa very faint to obsolete, anteroventrally tricarinate. Carapace tubercles low, rounded. Carapace with 4 prominent lateral carinae; anterior antennal (3rd) carina absent, posterior antennal carina usually with small anterior spine; anterior lateral (4th) carina expanded anteriorly into large vertically compressed, undivided lamina, apically acute, carapace width across tips of these spines slightly greater than

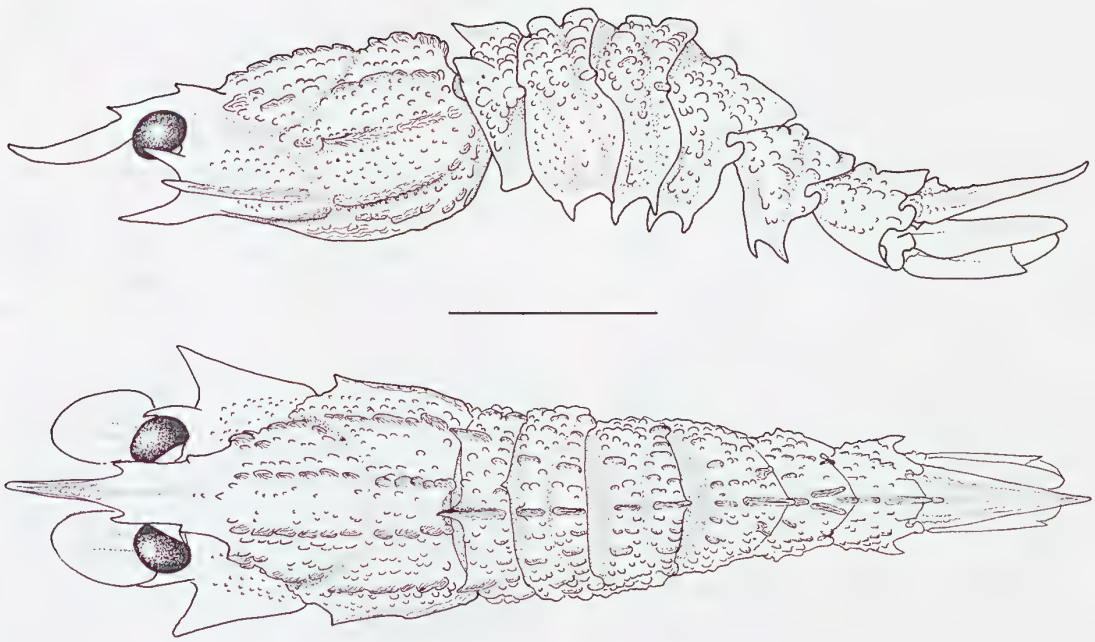

Fig. 24. *Glyphocrangon novacastellum* n.sp. Lateral and dorsal view. (Scale = 10 mm).

carapace length; tubercles of submedian carinae not laterally compressed, but broad and striate; tubercles between carinae low and blunt.

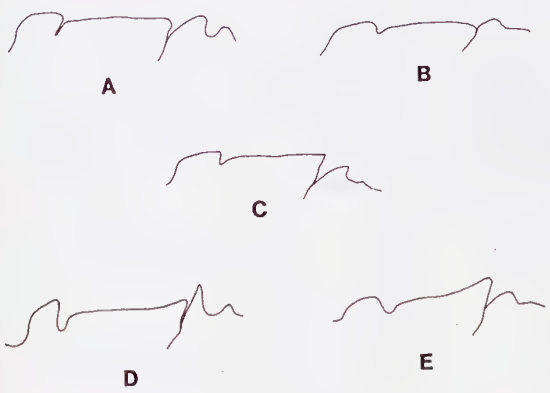

Fig. 25. Dorsal profile of pleonite 6 and anterior telson. **A,** *G. investigatoris,* Indonesia, USNM 205134; **B,** *G. regalis,* Indonesia, USNM 205128; **C,** *G. holthuisi,* paratype USNM 211397; **D,** *G. lowryi,* holotype AM P33158; **E,** *G. novacastellum,* paratype AM P26806.

Description. Integument weakly pubescent. Rostrum in adults about seven-tenths (0.68—0.75) carapace length, armed with 2 pairs of lateral teeth, anterior pair at about proximal two-fifths. Longitudinal ridge present along dorsal surface with transverse septa sometimes faintly present in anterior part but often indistinct. Longitudinal ridge also on ventral surface anteriorly, flanked by lateral ridges. Submedian (1st) carina composed of low subconical tubercles (not laterally compressed), directed obliquely forwards; anterior carina of 6 tubercles, posterior carina of 4 tubercles. Anterior intermediate (2nd) carina with first tubercle dentiform or subdentiform (as in submedian carina), remaining 3 or 4 tubercles low, sometimes indistinct. Posterior intermediate carina with 3—4 dentiform tubercles. Anterior antennal (3rd) carina absent. Posterior antennal (3rd) carina divided by 2, or occasionally 3, notches and armed with small acute spine anteriorly. Anterior lateral (4th) carina not continuous with branchiostegal spine, expanded into large vertically compressed, undivided lamina, directed forwards beyond level of posterior margin of orbit, apex acute and curved upwards slightly. Width across tips of these spines in adults equal to or usually greater (1.0—1.2) than carapace length. Posterior lateral carina entire or with 1 or 2, often shallow, notches, rarely

with 3 notches; usually unarmed, occasionally with small inconspicuous anterior tooth.

Tubercles between carapace carinae low, blunt, often in irregular rows. Row of tubercles midway between 3rd and 4th carinae with row of small, less distinct tubercles above and below. Carapace immediately posterior to eye smooth or with 1 or 2 small tubercles (occasionally up to 4 tubercles).

Antennal spine curved slightly mesially, smooth, about two-thirds (0.64—0.69) as long as branchiostegal spine. Tip of branchiostegal spine exceeding propod of pereopod 1 and reaching at least to end of penultimate segment of maxilliped 3.

Abdomen with median dorsal carinae on all somites. Somite 1 with anterior tubercles low; anterior height of dorsolateral carina greater than half and often subequal to basal length of carina. Somite 5 with 2 marginal spines on pleuron. Somite 6 with one posterior marginal spine on pleuron, directed slightly laterally with width across tips of these spines more than one and one-third (1.36—1.47) times anterior width of somite 6.

Telson with about one-fifth to one-quarter (0.18—0.29) of its length extending beyond apex of uropods.

Antennal scale more than one and one-half (1.62—1.77) times as long as broad. Maxilliped 3 extending as far as or very slightly beyond end of antennal peduncle. Pereopod 2 shorter on left hand side (20—21 carpal articles) than on right hand side (30—31, or 27 in juvenile, carpal articles). Length of pereopod 2 in relation to antennal scale seeming to vary with sex and age. Pereopod 2 on the LHS reaching about ⅔ of way along antennal scale in young specimen (cl 16 mm), not quite reaching to apex of scale in ovigerous females but slightly exceeding antennal scale in male of cl 23 mm. On RHS, pereopod 2 exceeding apex of antennal scale by chela and about 9 carpal articles in both male and ovigerous female but in specimen of cl 16 mm, only reaching apex of antennal scale. Pereopod 3 of ovigerous female reaching to end of antennal peduncle, i.e., nearly to end of antennal scale, pereopod 4 slightly shorter than 3, pereopod 5 reaching to end of propod of pereopod 4. In male of 23 mm (P19099), pereopod 3 extending past end of antennal peduncle and antennal scale; pereopod 4 slightly shorter than 3; pereopod 5 reaching halfway along propod of pereopod 4. On pereopods 3—5, propod about 1⅓X as long as carpus, dactyl between 2/5 and 3/5 length propod.

Colour. Colour in life white with orange markings. Antennae orange, also distal third of rostrum, spines around orbit, submedial and intermediate carinae and small tubercles between carinae. On abdomen, dorsal carinae, a few dorsal tubercles, and posterior dorsal margin of each segment orange, also telsonic submedian and marginal carinae.

Remarks. The three new species of *Glyphocrangon* described here have the following features in common: the anterior antennal carina is not continuous with the antennal spine; there are two pairs of lateral rostral teeth; the pleuron of abdominal somite 5 has two teeth; the anterior lateral carina is expanded into a vertically compressed acute lamina; the posterior antennal carina ends anteriorly in a small tooth, or lacks a tooth; the intercarinal areas are tuberculate; the eyes are pigmented. These features would place all three into the *G. regalis-G. investigatoris* group of species. (Chace (1984) notes that only one feature separates *G. smithii* from *G. regalis,* viz. the small acute tooth on the posterior antennal carina in the former, but expressed uncertainty about the constancy of this character). Table 7 summarises the differences between the three new species and *G. regalis* and *G. investigatoris.* The features used show considerable constancy for the number of specimens examined (which admittedly for *G. lowryi* is only one, but 25 and 229 for *G. novacastellum* and *G. holthuisi* respectively).

While some degree of uncertainty must be admitted regarding the validity of these new species, there would nevertheless seem to be a complex of at least five (or six) closely related taxa. By formally naming the three taxa separated here, attention is drawn to the differences. Future workers with more material available will thus be prompted to verify or demolish these findings.

Character	*G. regalis*	*G. investigatoris*	*G.holthuisi*	*G. lowryi*	*G. novacastellum*
Carapace integument	pubescent	glabrous	pubescent	glabrous	pubescent
Rostrum: dorsal septa	present, faint	present, strong	absent	present, fairly strong	present, faint
Rostrum: anteroventrum	tricarinate	flattened	tricarinate	bicarinate	tricarinate
Carapace: tubercles	rounded	rounded	acute, low	acute, flattened	rounded, low
Submedian carina: tubercles	broad, reticulate	broad, rounded	narrow	narrow, flattened	broad, striated
Posterior antennal carina	anteriorly with distinct tooth	anteriorly with right-angle	anteriorly with right-angle	anteriorly with strong tooth	anteriorly with small tooth
Dorsal profile, pleonite 6	see Fig. 25	see Fig. 25	see Fig. 25	see Fig. 25	see Fig. 25

Table 7. Comparison of five species in the *Glyphocrangon regalis* complex.

Etymology. The specific name is derived from Newcastle, the coastal city closest to the holotypic locality.

Family CRANGONIDAE

Pontocaris Bate, 1888

Pontocaris lacazei (Gourret)

Pontocaris lacazei.—Crosnier & Forest, 1973: 250, fig. 81; Chace, 1984: 42.

Material examined. New South Wales: AM P21031, north-east of Wollongong, 34°16—22′S 151°26—23′E, 356 m, demersal prawn trawl, *Kapala* (K75-05-01), 8 Aug 1975; 2 ♀. AM P5589, off Botany Bay, 34°00′S 151°11′E, 60—102 m, State Trawler *Goonambee,* Aug 1921; 2 ♀. AM P7864, off Botany Bay, 33°59′S 151°12′E, Trawler *Thistle,* Oct 1924; 1 ♀. AM P16278, off Cronulla, 100 m, dredged; 1 ♀. AM P24473, north-east of Brush Island, 35°30′S 151°48′E, 329 m, *Kapala* (K76-08-01), 8 June 1976; 1 ♀.

Diagnosis. Rostrum with one pair of basal teeth. Second lateral carine interrupted by hepatic groove. Median carina armed with 4 teeth. Tubercles absent between median and first lateral carina. Abdominal somite 4 with pair of dorsolateral carinae diverging posteriorly.

Distribution. Eastern Atlantic, Mediterranean, South Africa, Indo-Pacific to Philippines, Japan, Hawaii, New Zealand; 30—759 m.

Pontocaris rathbunae (de Man)

Aegeon Rathbunae de Man, 1918: 304; 1920: 300, pl. 24, fig. 74b, pl. 25, fig. 74a.
Pontocaris rathbunae.—Chace, 1984: 44.

Material examined. New South Wales: AM P28798, off Ulladulla, 35°30′S 150°48′E, 512 m, prawn trawl, *Kapala* (K79-11-06), 8 Aug 1979; 1 ♀. AM P20211, east to north-east of Port Jackson, 33°51′S 151°51′E to 33°45′S 151°55′E, 675 m, demersal prawn trawl, *Kapala* (K72-06-03), 19 Oct 1972; 1 ovig. ♀. AM P21782, south-east of Yamba, 29°41′S 153°45′E to 29°32′S 153°47′E, 403 m, demersal prawn trawl, *Kapala* (K75-09-04), 10 Oct 1975; 1 ovig. ♀.

Diagnosis. Rostrum with pair of basal teeth. Second lateral carina not interrupted by hepatic groove. Median carina with 5 teeth. No tubercles between median and first lateral carina. Abdominal somite 4 with 3 pairs of posterior diverging dorsolateral carinae.

Distribution. Off Indonesia, Hawaii; 11—1600 m.

Zoogeography

The present collection comprises 73 species of shrimps, almost all of which have come from depths ranging between 200 and 800 m. Some of these, such as the species of the genus *Gennadas,* are true pelagics, but the majority are benthic inhabitants. That 46 species (63%) should prove to be new records for the Australian fauna, is not surprising; as noted in the introduction, very little collecting at these depths has been done. That 11 undescribed species (15%) were encountered further illustrates the relatively unknown character of the fauna. Obviously, without further information on distribution, it is not possible to comment on the zoogeographical affinities of these new species. Several, such as the species of *Pasiphaea* and *Glyphocrangon* probably have distributions beyond the east coast of Australia; others such as the benthic *Lebbeus yaldwyni* probably have a more restricted range and could well be regarded as part of an endemic fauna.

The largest component of this fauna, seen from a zoogeographic viewpoint, is that which occurs in all the major oceans. This group of 32 species (five of which also occur in the Mediterranean Sea) includes most of the true mesopelagics as well as some of the deeper-dwelling benthics — 11 penaeoids, 12 species of oplophorids, two pasiphaeids, and four pandalids. To some extent, the composition of this group off New South Wales could have been predicted.

The next largest component of the fauna is a group of 27 species having an Indo-West Pacific distribution. These include 11 species of shallow- and bottom-dwelling penaeoids, e.g. *Solenocera* and *Hymenopenaeus,* and six species of pandalids. There may also be a southern subgroup in this component, as three species, viz. *Campylonotus rathbunae, Chlorotocus novaezeelandiae* and *Lipkius holthuisi,* have only been collected in the region of New Zealand and southern Australia.

The deepwater shrimp fauna off New South Wales would seem to be, in terms of composition and numbers, comparable to that of southern Africa (see Kensley, 1981b). About 90 deepwater shrimp species have been recorded from this region, which includes parts of both the southern Atlantic and south-western Indian ocean. Undoubtedly, further collecting would yield an even larger fauna off New South Wales, given that this region is close to centers of high diversity such as those around the Philippines and Indonesia.

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References

Alcock, A., 1901. A descriptive catalogue of the Indian deep-sea Crustacea Decapoda Macrura and Anomala, in the Indian Museum. Being a revised account of the deep-sea species collected by the Royal Indian Marine Survey ship *Investigator*. Calcutta: Indian Museum, 286 pp.

Alcock, A. & A.R. Anderson. 1894. Natural History Notes from H.M. Indian Marine Survey steamer 'Investigator', Commander C.F. Oldham, R.N., commanding. Series II, No. 14. An account of a recent collection of deep-sea Crustacea from the Bay of Bengal and Laccadive Sea. Journal of the Asiatic Society of Bengal 63 (II—3): 141—185.

———— 1899. Natural History Notes from H.M. Royal Indian Marine Survey ship 'Investigator', Commander T.H. Heming, R.N., commanding. Series III, No. 2. An account of the deep-sea Crustacea dredged during the surveying-season of 1897—98. Annals and Magazine of Natural History (7)3: 1—27, 278—292.

Alcock, A. & A.F. McArdle, 1901. Crustacea. Part 9. Illustrations of the Zoology of the Royal Indian Marine Survey ship *Investigator*, under the command of Captain T.H. Heming, R.N. (Retired), plates 49—55. Calcutta.

Anderson, A.R.S., 1896. Natural history notes from the R.I.M. Survey steamer 'Investigator', Commander C.F. Oldham, R.N., commanding. Series II, No. 21. An account of the deep sea Crustacea collected during the season 1894—95. Journal of the Asiatic Society of Bengal 65(II—2): 88—106.

Balss, H., 1927. Macrura der Deutschen Tiefsee-Expedition. 3. Natantia, Teil B. Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition 'Valdivia' 23: 245—275.

Barnard, K.H., 1950. Descriptive catalogue of South African decapod Crustacea (crabs and shrimps). Annals of the South African Museum 38: 1—837.

Bate, C.S., 1881. On the Penaeidea. Annals and Magazine of Natural History (5)8: 169—195.

Bate, C.S., 1888. Report on the Crustacea Macrura collected by H.M.S. Challenger during the years 1873—1876. Report of the Voyage of the Challenger 1873—1876, 24: 1—942.

Borradaile, L.A., 1899. On the Stomatopoda and Macrura brought by Dr Willey from the South Seas. **In** Willey, Zoological results based on material from New Britain, New Guinea, Loyalty Islands and elsewhere, collected during the years 1895, 1896, and 1897, 4: 395—428.

———— 1916. Crustacea, Part 1.—Decapoda. British Antarctic ("Terra Nova") Expedition, 1910. Natural History Report. Zoology 3(2): 75—110.

Bouvier, E.L., 1905. Sur les Peneides et les Stenopides recueillis par les expéditions francaises et monegasques dans l'Atlantique oriental. Comptes rendus hebdomadaires des Séances de l'Académie de Sciences, Paris 140: 980—983.

———— 1906. Suite aux observations sur les *Gennadas* ou Peneides bathypelagiques. Comptes rendus hebdomadaires des Séances de l'Académie des Sciences, Paris 142: 746—749.

Brandt, J.F., 1851. Krebse. **In** Middendorff's Reise in den aussersten Norden und Osten Sibiriens 2(1): 79—148.

Brashnikov, V., 1907. Beiträge zur Fauna der russischen ostlichen Meere, gesammeltvon dem Schoner "Storosh" in die Jare 1899—1902. Memoires de l'Académie des Sciences, St. Petersburg ser. 8 20(6): 1—185.

Bruce, A.J., 1966. *Hymenopenaeus halli* sp. nov., a new species of penaeid prawn from the South China Sea (Decapoda, Penaeidae). Crustaceana 11(2): 216—224.

Brullé, M., 1839. Crustaces. **In** Webb and Berthelot: Histoire Naturelle des Îles Canaries 2(2): 15—18.

Calman, W.T., 1925. On macrurous decapod Crustacea collected in South African waters by the S.S. 'Pickle'. Report of the Fisheries and Marine Biological Survey of the Union of South Africa 4 (special report 3): 1—26.

———— 1939. Crustacea Caridea. Scientific Reports of the John Murray Expedition 1933—34, 6(4): 183—224.

Casanova, J.-P., 1976. Crustacés Decapodes pelagiques de la province Atlanto-Mediterranéene — Notes taxonomiques et biogeographiques. Rapports de la Commission internationale pour l'Exploration scientifique de la Mer Mediterranée 23 (9): 63—64.

Casanova, J.-P. & D.C. Judkins, 1977. Les décapodes pelagiques en Mediterannée. Répartition et secteurs faunistiques. Rapports de la Commisssion internationale pour l'Exploration scientifiques de la Mer Mediterranée 24(10): 125—127.

Chace, F.A. Jr., 1940. Plankton of the Bermuda Oceanographic Expeditions. 9. The bathypelagic caridean Crustacea. Zoologica New York 25(2): 117—209.

———— 1983. The caridean shrimps (Crustacea: Decapoda) of the *Albatross* Philippine Expedition, 1907—1910, Part 1: Family Stylodactylidae. Smithsonian Contributions to Zoology 381: i-iii, 1—21.

———— 1984. The caridean shrimps (Crustacea: Decapoda) of the *Albatross* Philippine Expedition, 1907—1910, Part 2: Families Glyphocrangonidae and Crangonidae. Smithsonian Contributions to Zoology 397: i-iv, 1—63.

———— 1985. The caridean shrimps (Crustacea: Decapoda) of the *Albatross* Philippine Expedition, 1907—1910, Part 3: Families Thalassocarididae and Pandalidae. Smithsonian Contributions to Zoology 411: 1—143.

———— 1986. The caridean shrimps (Crustacea: Decapoda) of the *Albatross* Philippine Expedition, 1907-1910, Part 4: Families Oplophoridae and Nematocarcinidae. Smithsonian Contributions to Zoology 432: i-iv, 1—82.

Coutière, H. 1905. Sur quelques Crustacés provenant des campagnes de la *Princesse-Alice* (Filet à grande ouverture). Comptes rendus hebdomadaires des Séances de l'Académie des Sciences, Paris 140: 1113—1115.

Crosnier, A. 1970. Crustacés décapodes brachyoures et macroures recueillis par l'"Undaunted" au sud de l'Angola. Description de *Scyllarus subarctus* sp. nov. Bulletin du Muséum National d'Histoire Naturelle, Paris (2) 41(5): 1214—1227.

_____ 1976. Donnees sur les crustaces decapodes captures par M. Paul Gueze a l'Île Réunion lors d'essais de peche en eau profonde. Travaux et Documents ORSTOM 47: 225—256.

_____ 1978. Crustacés Décapodes Peneides Aristeidae (Benthesicyminae, Aristeinae, Solenocerinae). Faune de Madagascar 46: 1—197.

_____ 1985a. Crustacés Décapodes: Penaeidae. Les especes indo-pacifiques du genre *Parapenaeus*. Resultats des Campagnes Musorstom I et II. Memoires du Muséum national d'Histoire naturelle, Paris ser. A, Zoologie 133: 303—353.

_____ 1985b. Crevettes pénéides d'eau profonde recoltées dans l'océan Indien lors des campagnes BENTHEDI, SAFARI I et II, MD 32/RÉUNION. Bulletin du Muséum National d'Histoire Naturelle, serie 4, Section A, Tome 7, no. 4: 839—877.

Crosnier, A. & J. Forest, 1973. Les crevettes profondes de l'Atlantique oriental tropical. Faune Tropicale 19: 1—409.

Dall, W., 1957. A revision of the Australian species of Penaeinae (Crustacea Decapoda: Penaeidae). Australian Journal of Marine and Freshwater Research 8(2): 136—230.

Fabricius, J.C., 1798. Supplementum Entomologiae Systematicae. Copenhagen.

Figueira, A.J.G., 1971. Materials for a revision of the family Stylodactylidae (Crustacea Decapoda: Caridea) 1. Description of a new genus and of a new species. Arquivos do Museu Bocage ser. 2, 3(1): 1—8.

Gourret, P., 1887. Sur quelques Décapodes macroures nouveaux de Golfe de Marseille. Comptes rendus de l'Académie des Séances de la Sciences, Paris 105: 1033—1035.

Grey, D.L., W. Dall & A. Baker, 1983. A Guide to the Australian Penaeid Prawns. Darwin: Northern Territory Government Printing Office. 140 pp.

Griffiths, F.B. & S.B. Brandt, 1983. Mesopelagic Crustacea in and around a Warm-core Eddy in the Tasman Sea off Eastern Australia Australian Journal of Marine and Freshwater Research 34: 609—623.

Hall, D.N.F., 1956. The Malayan Penaeidae (Crustacea, Decapoda). Part 1. Introductory notes on the species of the genera Solenocera, Penaeus and Metapenaeus. Bulletin of the Raffles Museum 27: 68—90.

_____ 1962. Observations on the taxonomy and biology of some Indo-West Pacific Penaeidae (Crustacea, Decapoda). Colonial Office, Fisheries Publications No. 17. Her Majesty's Stationery Office, London. 229 pp.

Hayashi, K.-I. & S. Miyake, 1969. Bathypelagic caridean shrimps collected by "Koyo Maru" during the International Indian Ocean Expedition. OHMU 2(4): 59—77.

Holthuis, L.B, 1947. Nomenclatural notes on European macrurous Crustacea Decapoda. Zoologische Mededeelingen 27: 312—322.

_____ 1949. The Caridean Crustacea of the Canary Islands. Zoologische Mededeelingen 30: 227—255.

_____ 1951. The caridean Crustacea of tropical West Africa. Atlantide Report 2: 7—187.

_____ 1955. The recent genera of the caridean and stenopodidean shrimps (Class Crustacea, Order Decapoda, Supersection Natantia) with keys for their determination. Zoologische Verhandelingen 26: 1—157.

_____ 1961. A new species of *Merhippolyte* (Decapoda Natantia) from east American waters. Crustaceana 2: 1—5.

Holthuis, L.B. and E. Sivertsen, 1967. The Crustacea Decapoda, Mysidacea and Cirripedia of the Tristan da Cunha Archipelago, with a revision of the *"frontalis"* subgroup of the genus *Jasus*. Results of the Norwegian Scientific Expedition to Tristan da Cunha 1937—1938, 52: 1—55.

Johnson, J.Y., 1867. Description of a new genus and a new species of macrurous decapod crustaceans, belonging to the Penaeidae, discovered at Madeira. Proceedings of the Zoological Society of London 1867: 895—901.

Kemp, S., 1906. On the occurrence of the genus *Acanthephyra* in deep water off the west coast of Ireland. Department of Agriculture and Technical Instruction for Ireland. Fisheries Branch. Scientific Investigations 1905, 1: 1—28.

_____ 1909. The decapods of the genus *Gennadas* collected by H.M.S. 'Challenger'. Proceedings of the Zoological Society of London 11: 718—730.

_____ 1913. Pelagic Crustacea Decapoda of the Percy Sladen Trust Expedition in H.M.S. "Sealark". Transactions of the Linnean Society of London (2) Zoology 16: 53—68.

000001939. On *Acanthephyra purpurea* and its allies (Crustacea, Decapoda, Hoplophoridae). Annals and Magazine of Natural History (11)4: 568—579.

Kemp, S. & R.B.S. Sewell, 1912. Notes on Decapoda in the Indian Museum, III. Records of the Indian Museum 7(1): 15—32.

Kensley, B., 1968. Deep sea decapod Crustacea from west of Cape Point, South Africa. Annals of the South African Museum 50(12): 283—323.

_____ 1971. The genus *Gennadas* in the waters around southern Africa. Annals of the South African Museum 57(12): 271—294.

_____ 1972. Shrimps and prawns of southern Africa. South African Museum, Cape Town. 65 pp.

_____ 1977. The South African Museum's *Meiring Naude* cruises. Part 5. Crustacea, Decapoda, Reptantia and Natantia. Annals of the South African Museum 74(2): 13—44.

_____ 1981a. The South African Museum's *Meiring Naude* cruises. Part 12. Crustacea Decapoda of the 1977, 1978, and 1979 cruises. Annals of the South African Museum 83(4): 49—78.

_____ 1981b. On the zoogeography of southern African Decapod Crustacea, with a checklist of the species. Smithsonian Contributions to Zoology 338: i-iii, 1—64.

Kubo, I., 1937. One new and an imperfectly known deep-sea shrimps. Journal of the Imperial Fisheries Institute, Tokyo 32: 93—103.

_____ 1942. On two new species of Decapoda Macrura. Annotationes Zoologicae Japonensis 21(1): 30—38.

_____ 1943. Diagnosis of a new species of the genus *Penaeus*. Suisan Kenkyusi 38(11): 200—201.

_____ 1949. Studies on penaeids of Japanese and its adjacent waters. Journal of the Tokyo College of Fisheries 36(1): 1—467.

Lucas, H., 1849. Observations sur un nouveau genre de l'ordre des decapodes (Solenocera, Philippi, Luc.).

Annales de la Société Entomologique, Paris (2)8: 215—224.

MacPherson, E. 1984. Crustáceos Decápodos del Banco Valdivia (Atlántico sudoriental). Resultados Expediciones Científicas 12: 39—105.

Man, J.G. de, 1907. Diagnoses of new species of macrurous decapod Crustacea from the "Siboga Expedition". Notes from the Leyden Museum 29(2): 127—146.

_____ 1911. The Decapoda of the Siboga Expedition. Part 1. Family Penaeidae. Siboga Expeditie, monographie 39a: 1—131.

_____ 1917. Diagnoses of new species of macrurous decapod Crustacea from the Siboga-Expedition. Zoologische Mededeelingen Leiden 3(4): 279—284.

_____ 1918. Diagnoses of new species of macrurous decapod Crustacea from the Siboga-Expedition. Zoologische Mededeelingen Leiden 4(3): 159—166.

_____ 1920. The Decapoda of the Siboga Expedition. Part 4. Families Pasiphaeidae, Stylodactylidae, Hoplophoridae, Nematocarcinidae, Thalassocaridae, Pandalidae, Psalidopodidae, Gnathophyllidae, Processidae, Glyphocrangonidae, and Crangonidae. Siboga-Expeditie monographie, 39a3: 1—318.

Man, J.G. 1931. On a new species of the genus *Hoplophorus (Oplophorus)* H.M. Edw., *Hoplophorus novae-zealandiae,* sp. n. Journal of the Linnean Society of London 37: 369—378.

Milne Edwards, A., 1881. Description quelques Crustacés macroures provenant des grandes profondeurs de la Mer des Antilles. Annales des Sciences Naturelles, Zoologie (6) 11(4): 1—16.

_____ 1882. Rapport sur les travaux de la Commission chargée d'etudier la faune sous-marine dans les grandes profondeurs de la Mediterranée et de l'ocean Atlantique. Archives des Missions scientifique et Litteraires (3)9: 1—59.

_____ 1883. Recuiel de figures de Crustaces nouveaux ou peu connus, 3 pp., 44 pls.

Milne Edwards, H., 1837. Histoire Naturelle des Crustaces Vol. 2, 531 pp. Librairie Encyclopedique de Roret, Paris.

Nataraj, S., 1945. On two species of *Solenocera* (Crustacea Decapoda: Penaeidae) with notes on *Solenocera pectinata* (Spence Bate). Journal of the Asiatic Society of Bengal 11(1): 91—98.

Pérez Farfante, I., 1977. American solenocerid shrimps of the genera *Hymenopenaeus, Haliporoides, Pleoticus, Hadropenaeus* new genus and *Mesopenaeus* new genus. United States Fisheries Bulletin 75(2): 261—346.

_____ 1977. *Penaeopsis eduardoi,* a new species of shrimp (Crustacea: Penaeidae) from the Indo-West Pacific. Proceedings of the Biological Society of Washington 90(1): 172—182.

Pérez Farfante, I. & B. Kensley, 1985. *Cryptopenaeus crosnieri,* a new species of shrimp, and a new record of *C. sinensis* (Penaeoidea: Solenoceridae) from Australian waters. Proceedings of the Biological Society of Washington 98(1): 281—287.

Potter, M.A. & M.C.L. Dredge, 1985. Deepwater Prawn resources off southern and central Queensland. Pp. 221—229, **in** P.C. Rothlisberg, B.J. Hill & D.J. Staples (eds), Second Australian National Prawn Seminar, NPS2, Cleveland, Queensland, Australia.

Racek, A.A. & W. Dall, 1965. Littoral Penaeinae (Crustacea Decapoda) from Northern Australia, New Guinea and Adjacent Waters. Verhandelingen der Koninglijke Nederlandse Akademie van Wetenschappen, Afd. Natuurkunde (2) 56(3): 1—116.

Ramadan, M.M., 1938. Crustacea, Penaeidae. Scientific Reports of the John Murray Expedition 5: 35—76.

Rathbun, M.J., 1906. The Brachyura and Macrura of the Hawaiian Islands. Bulletin of the United States Fish Commission 23(3): 827—930.

_____ 1902. Descriptions of new decapod crustaceans from the west coast of North America. Proceedings of the United States National Museum 24: 885—905.

Risso, A., 1816. Histoire naturelle des crustaces des environs de Nice. 1—175. Librairie Grecque-Latine-Allemande, Paris.

_____ 1827. Histoire naturelle des principales productions de l'Europe meridionale et particulierement de celles des environs de Nice et des Alpes-Maritimes 5, (I-VIII): 1—403.

Sabine, E., 1824. Invertebrate Animals. **In** W.E. Parry, 'Journal of a Voyage for the Discovery of a Northwest Passage from the Atlantic to the Pacific; Performed in the Years 1819—20 in His Majesty's Ships *Hecla* and *Griper'* pp 219—239. J. Murray, London.

Schmitt, W.L., 1926. Report on the Crustacea Macrura (Families Peneidae, Campylonotidae, and Pandalidae) obtained by the F.I.S. "Endeavour" in Australian seas. Biological Results of the Fishing Experiments carried on by the F.I.S. "Endeavour" 1909—14, 5(6): 311—381.

Smith, S.I., 1882. Report on the Crustacea. Part 1. Decapoda. Reports on the results of dredging, under the supervision of Alexander Agassiz, on the east coast of the United States, during the summer of 1880, by the U.S. Coast Survey Steamer "Blake", Commander J.R. Bartlett, U.S.N., commanding. Bulletin of the Museum of Comparative Zoology at Harvard College 10(1): 1—108.

_____ 1884. Report on the decapod Crustacea of the Albatross dredgings off the east coast of the United States in 1883. Report of the United States Fish Commission 10: 345—426.

_____ 1885. On some new or little known decapod Crustacea, from recent Fish Commission dredgings off the east coast of the United States. Proceedings of the United States National Museum 7: 493—511.

_____ 1886. The abyssal decapod Crustacea of the 'Albatross' dredgings in the North Atlantic. Annals and Magazine of Natural History (5)17: 187—198.

Stebbing, T.R.R., 1914. South African Crustacea. Annals of the South African Museum 15: 1—55.

Suseelan, C. & K.H. Mohamed, 1969. On the occurrence of *Plesionika ensis* (A. Milne Edwards) (Pandalidae, Crustacea) in the Arabian Sea with notes on its biology and fisheries potentialities. Journal of the Marine Biological Association of India 10(1): 88—94.

Thompson, J.R., 1966. The caridean superfamily Bresilioidea (Decapoda Natantia). A revision and a discussion of its validity and affinities. Crustaceana 11(2): 129—140.

White, A., 1847. List of the specimens of Crustacea in the collection of the British Museum. British Museum, London, 143 pp.

Wicksten, M.K. & M. Mendez, 1982. New records and new species of the genus *Lebbeus* (Caridea: Hippolytidae) in the Eastern Pacific Ocean 81(3): 106—120.

Wood Mason, J. & A. Alcock, 1891. Natural history notes from H.M. Indian Marine Survey steamer 'Investigator', Commander R.F. Hoskyn, commanding.

Series II. No. 21. Note on the results of the last season's deep-sea dredging. Annals and Magazine of Natural History (6)7: 186—202.

_____ 1892. Natural history notes from H. M. Indian Marine Survey steamer 'Investigator', Commander R. F. Hoskyn, R.N., commanding. Series II. No. 1. On the results of deep-sea dredging during the season 1890—91. Annals and Magazine of Natural History (6)9: 358—370.

_____ 1893. Natural History notes from H.M. Indian Marine Survey steamer 'Investigator', Commander R.F. Hoskyn, R.N., commanding. Series II. No. 1. On the results of deep-sea dredging during the season 1890—91. Annals and Magazine of Natural History (6)11: 161—172.

Yaldwyn, J.C., 1960. Biological results of the Chatham Islands 1954 Expedition. Part 1. Crustacea Decapoda Natantia from the Chatham Rise: a deep water bottom fauna from New Zealand. Bulletin of the New Zealand Department of Scientific and Industrial Research 139(1): 13—53.

_____ 1967. A summary of the composition and relationships of the New Zealand macruran and anomuran fauna. Australian-New Zealand Meeting on Decapod Crustacea, Sydney October 24—28, 1967. 7 pp.

_____ 1971. Preliminary descriptions of a new genus and twelve new species of natant decapod Crustacea from New Zealand. Records of the Dominion Museum, Wellington 7(10): 85—94.

Yokoya, Y., 1933. On the Distribution of Decapod Crustaceans inhabiting the Continental Shelf around Japan, chiefly based upon the Materials collected by S.S. Soyo-Maru, during the Year 1923—1930. Journal of the College of Agriculture, Tokyo Imperial University 12: 1—226.

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The Genus *Nyctimystes* (Anura: Hylidae) in Australia

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ABSTRACT. Three species of hylid frogs of the genus *Nyctimystes* have been reported from Australia. With evidence from morphology and field work, we conclude there is only one species. The earliest available name for this taxon is *Hyla dayi* Günther 1897, the holotype of which is missing. We refer the species to *Nyctimystes* and, to stabilise the nomenclature, we designate a neotype.

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Since Tyler (1968), it has been generally accepted that there are three species of *Nyctimystes* in Australia: *N. hosmeri, N. tympancryptis* and *N. vestigea* (e.g. Barker & Grigg, 1977; Cogger, 1983; Cogger *et al.,* 1983). Our field observations in northeast Queensland — at the type localities and others — suggested that there was only one Australian species. An examination of a large series of preserved material, including all extant types, confirmed our suspicions: we found continuous variation in all characters previously thought to be diagnostic of the three species.

Measurements are given in millimetres and ratios are expressed as percentages. The following standard abbreviations are used: SV, snout-vent length; HW, width of the head at the broadest part; HL, distance from the tip of the snout to the middle of the head above the angle of the jaws; EN, distance between the external nostril and anterior border of eye; IN, distance between two external nostrils; ED, diameter of the eye between anterior and posterior borders; IO, interorbital width at narrowest part of frontoparietal; TW, tympanum width; TL, tibial length. Description of webbing on hands and feet follows the formula of Schiøtz (1967). Specimens examined are housed in the Australian Museum (AM), Queensland Museum (QM), American Museum of Natural History (AMNH), Rijksmuseum van Natuurlijke Historie (RMNH), and Naturhistorisches Museum, Wien (NHMW).

HISTORY

The nomenclatural history of the Australian frogs presently assigned to *Nyctimystes* is complex. There are two separate issues: 1. the number of species of *Nyctimystes,* and 2. the identity of *Hyla dayi.* Günther (1897) described a frog, *Hyla dayi,* from Bartle Frere Mountains, NE Queensland — the holotype of which has not been located subsequently (Tyler, 1968; Liem, 1974; Duellman, 1977; Cogger *et al.,* 1983). Andersson (1916) described *Hyla tympanocryptis* from Malanda on the Atherton Tableland near Mt Bartle Frere. Loveridge (1935) and Copland (1957) considered these names to be synonymous but both noted problems with the identity of the name-bearing specimen of *Hyla dayi.* Even so, they referred specimens to a taxon of that name. Tyler (1964) first noted the presence of the genus *Nyctimystes* in Australia and described two new species: *Nyctimystes hosmeri* from Tully Falls on the southern edge of the Atherton Tablelands, and *N. vestigea* from Mt Bartle Frere. (Cogger *et al.* [1983] gave the name as "*vestigia*". It was spelt "*vestigia*" in the header to Tyler's description, but this was obviously a printing error. In the text, and in later papers, Tyler used "*vestigea*"). Tyler (1968) showed that *Hyla tympanocryptis* was a *Nyctimystes* and stated that it was a valid species separable from both *N. hosmeri* and *N. vestigea.* He also noted difficulties with the identity of *Hyla dayi.* There were differences between the description of the holotype and the frogs

Loveridge (1935) and Copland (1957) had referred to this name. For practical purposes, Tyler decided that there was justification for considering the differences unimportant.

Liem (1974) studied the differences between the type description of *Hyla dayi* and members of the *Litoria nannotis* species group. He was convinced that *Hyla dayi* referred to an indeterminate species of *Nyctimystes,* while the frogs traditionally referred to *Hyla dayi* were a new species: these he described as *Litoria rheocolus.* Liem left the identity of the name-bearing specimen of *Hyla dayi* in abeyance because the type description did not have enough detail to assign it to any *Nyctimystes.* Cogger (1975), Tyler (1976), Duellman (1977), Tyler & Davies (1978, 1979), and Ingram & Covacevich (1981) accepted Liem's decisions. Barker & Grigg (1977), however, while listing Liem's (1974) paper, did not use his new name. Instead, they used *Litoria dayi* in the traditional sense of *Hyla dayi.* Duellman (1977, 1985) apparently accepted Liem's argument, but went further. He listed a fourth species of *Nyctimystes* from Australia: *N. dayi.*

SPECIES

Even though three species of *Nyctimystes* in Australia have been generally accepted, some doubts have been raised about the validity of the taxa. Grigg & Barker (1977) said there was little to distinguish *N. tympanocryptis* from *N. hosmeri.* Cogger (1975) said that the status of one or two of the species is doubtful; he also thought that *N. tympanocryptis* was closely allied to *N. vestigea.* Liem (1974) said he intended to discuss the validity of *vestigea* in a subsequent paper.

In the field, we have heard little difference among the breeding calls of *Nyctimystes* throughout north-east Queensland. We have also visited the type localities of the purported three species. Further, using the keys in both Cogger (1975) and Grigg & Barker (1977), we have identified the three 'species' giving the same call: even within the one chorus. Also, there were many individuals that were impossible to key out. They exhibited character states that proved intermediate between the diagnostic characters given by the various authors. From our field experience, we thought it likely that there was only one species. To test this, we examined a large number of spirit specimens.

N. hosmeri purportedly differed from *N. vestigea* in palpebral venation (thick recticulum *vs* fine lines), dorsal colouration of head and body (dark brown with large cream spots *vs* light brown), and webbing of the fingers (one-half webbed *vs* two-thirds webbed) (Tyler, 1964). It should be noted that, at the time, only one specimen of each of the taxa were available. Since then, many more specimens have been collected. This paper is based upon 167 males and seven females. An examination of these show that the palpebral venation is always reticulated, and there is continuous variation in the intensity of the colour. One specimen (QM J25219) exhibits the extremes of the variation; one eyelid has an 'open' reticulum, the other has a dense one. Dorsal colouration varies from brown, through grey, to grey-green and cream; brown or white spots may be absent, and, if present, vary in size. The webbing on the fingers varies from half to two-thirds webbed. This intraspecific variation in webbing is not unusual (for example, *Litoria rheocola* and *L. nyakalensis* in Liem, 1974).

The striking differences between *N. tympanocryptis* and *N. vestigea* were in the shape of the head (triangular and subacuminate *vs* tip of snout evenly rounded) and the prominence of the eye (ED<EN *vs* ED>EN) (Tyler, 1968). This was based upon one female specimen of *N. tympanocryptis* and three of *N. vestigea.* In the specimens we examined, there is continuous variation from an acuminate snout to a rounded one. Also, we found that ED was always greater than EN (our specimens also included the holotype of *tympanocryptis).* There were other diagnostic characters that purportedly separated *N. tympanocryptis* from both *N. hosmeri* and *N. vestigea* (Tyler *loc. cit.,* Table 1). The more important of these, which also are used in the first couplet of Cogger's (1975) key, are the obviousness of the tympanum (invisible externally *vs* visible) and the dermal fold on the heel (large *vs* absent, or small if present). We have found that in all specimens the tympanum is covered by skin, but the tympanic annulus may be obscure to distinct. Furthermore, the outward appearance of the ear may be altered by preservation. If a specimen is set in a strong fixative, the tympanic annulus can become more prominent. Of the dermal fold on the heel, it may be absent, be present as a series of low tubercles, or be more fully developed as a distinct fold.

From these examinations, we are convinced that there is only one species of *Nyctimystes* in Australia. We accept Liem's (1974) argument that the name-bearing specimen of *Hyla dayi* is a *Nyctimystes.* Therefore it is the earliest available name for the Australian species. But, as can be seen from the foregoing, there is a difficulty with the name '*Hyla dayi*' — it has been applied as a valid name several times. To avoid instability of the nomenclature, we have selected NHMW 17187 as the neotype of *Hyla dayi* Günther, 1897. This specimen is also the holotype of *Nyctimystes vestigea* Tyler (1964). Tyler provided a description of the specimen (p. 113) and an illustration (pl. 1). The specimen came from Mt Bartle Frere, which we have assumed in the same locality as the "Bartle Frere Mountains" of Günther. We think it appropriate to choose one of Tyler's specimens because the selection acknowledges his contribution towards elucidating this difficult genus of frogs.

Nyctimystes dayi (Günther)

Hyla dayi Günther, 1897: 406. Mt Bartle Frere, north-east Queensland. Neotype NHMW 17187 (here designated).

Hyla tympanocryptis Andersson, 1916: 19. Malanda, north-east Queensland. Holotype RMNH 1649.

Nyctimystes hosmeri Tyler, 1964: 111. Tully Falls, north-east Queensland. Holotype AMNH 65538.

Nyctimystes vestigea Tyler, 1964: 113. Mt Bartle Frere, north-east Queensland. Holotype NHMW 17187.

Material examined. Home Rule (QM J24857); Wallaby Creek, Home Rule, south of Cooktown (QM J25147-50, J25219); Home Rule Falls (QM J25261-2); Slaty Creek, Home Rule (AM R26778-9); The Granites, Home Rule, 30 km south of Cooktown (QM J25277); Little Forks, near Shiptons Flat (QM J27151, J27163, J27259); Bloomfield River (QM J36324-5); Cape Tribulation (QM J36323, J36326-9); Mulgrave River (QM J30905-6, J30908-12, J32068, J32091, J32096, J32101-2, J32130, J32166, J32168); Upper Russell River, west slope Mt Bartle Frere (AM R61388): Headwaters of Russel River, near base of Mt Bartle Frere (QM J30914, J32072, J32093-4, J32099, J32113, J32119, J32119, J32124, J32133-4, J32170-2); Mt Bartle Frere (NHMW 17187); Atherton (AM R39722); The Boulders, via Babinda (QM J36330-1); Malanda (RMNH 1649); The Crater (QM J24529); Mt Hypipamee (QM J24530); Dinner Falls, The Crater (AM R53954), Atherton-Ravenshoe road near The Crater National Park (QM J29524-5, J30700, J30917-9, J32095); 6 km east of The Crater on Atherton-Ravenshoe road (QM J32164-5); Atherton Tableland (QM J25080, J25085); 34 km west of Innisfail (QM J29717-24); Palmerston Highway, near Milla Milla (QM J31966, J32066-7, J32080, J32098, J32131-2, J32139); Boulder Creek, Palmerston National Park (QM J36314, J36315-7, J36338-47); Henrietta Creek, Palmerston National Park (QM J25570-1, J36332-7); Maalan State Forest (QM J31181); McHugh Bridge, approx 42.8 km E. of Ravenshoe (QM J29670-6); Tully Falls (AMNH 65538, QM J29258, J32065, J32092, J32100, J32169, J32174, J36308, J36312-3, J36321-2); Koombooloomba Dam (QM J29559-62, J29573-5); Mt Spec, via Paluma (QM J36309-11, J36318-9); Paluma (QM J29593-6, J30899, J32097, J32122, J32173).

Diagnosis. *Nyctimystes dayi* may be readily distinguished from all other Australian frogs by the presence of a palpebral venation.

Description and variation. One hundred and sixty-seven males: SV, 30—42 ($\bar{x}$ = 34.6); TL/SV, 49—65 ($\bar{x}$ = 56.8); HW/SV, 28—40 ($\bar{x}$ = 35.6); IO/IN, 103—192 ($\bar{x}$ = 134.8); HW/HL, 90—112 ($\bar{x}$ = 101.1); EN/IN, 106—149 ($\bar{x}$ = 128.1); ED/EN, 106—152 ($\bar{x}$ = 127.4); TW/ED, 29—40 ($\bar{x}$ = 34.2). Seven females: SV, 45—55 ($\bar{x}$ = 49.4); TL/SV, 52—58 ($\bar{x}$ = 54.7); HW/SV, 31—37 ($\bar{x}$ = 34.9); IO/IN, 127—156 ($\bar{x}$ = 134.6); HW/HL, 105—110 ($\bar{x}$ = 107.3); EN/IN, 117—131 ($\bar{x}$ = 124.5); ED/EN, 107—126 ($\bar{x}$ = 117.2); TW/ED, 31—41 ($\bar{x}$ = 35.6).

Figure 1. *N. dayi*, Wallaby Creek, South of Cooktown, NEQ.

Eye large and prominent. Iris dark brown in life. Pupil vertically elliptical.

Snout shape variable, ranging from acuminate to rounded. The former condition is more common in northern populations. Canthus rostralis prominent, usually straight, but may be slightly curved in females. Loreal region sloping to slightly concave. Tympanum is covered by skin. The tympanic annulus may be obscure or prominent; this character is often altered by method of preservation. Supratympanic fold present, often obscuring anterior margin of tympanum. Palpebral venation subject to both individual and population variation, as well as method of preservation; brown to pearl to silver in colour, forming moderately dense to dense reticula that are mostly vertically oriented. Numerous short horizontal connections may be present; if these are absent, the reticulum is 'open' and consists of a few vertical lines. One specimen (QM J25219) exhibits both degrees of density.

Vomerine tooth rows in 2 separate oval series posterior to choanae; rarely touching medially. One specimen (QM J32169) with only 1 row.

Subarticular tubercles on hand rounded, 1 each on first and second fingers and 2 each on third and fourth fingers; 1 outer metacarpal tubercle (rarely reduced or absent). Subarticular tubercles on feet rounded. One each on first and second toe, 2 on third toe, 2—3 on fourth and fifth toes with the third tubercle, when present, poorly defined. Two metatarsal tubercles, outer small; inner elongated and rarely absent.

Distinct dermal flap may be present on the heel or absent and replaced by 2—3 low tubercles. Series of tubercles also present along posterior margin of tarsus. Distinct, usually prominent fold along posterior margin of forelimb; series of tubercles present along humeral fold, giving posterior margins of limbs serrated, crenulated or scalloped appearance.

Hands moderately webbed: 1 (1½—1⅔), 2i (1½—1⅔), 2e (0—½), 3i (1½—2), 3e (1), 4 (1). Feet extensively webbed: 1 (0—⅔), 2i (0—1½), 2e (0), 3i (0—½), 3e (0—⅓), 4i (½—1), 4e (½—1), 5 (0). Toe discs subequal to slightly smaller than finger discs.

Dorsal surface of skin, shagreened, finely granular to smooth; ventral surfaces coarsely granular.

Colouration and pattern of dorsum variable (see Figs 1,2). Dorsum may be: 1. uniform brown, 2. brown with irregular light brown markings, 3. brown with cream reticulations, 4. uniform grey-brown, 5. fawn-brown with dark brown spots, 6. grey with dark brown spots, 7. cream, 8. grey with white spots that may have black centres, 9. brown with white spots that may have black centres, 10. uniform reddish brown, 11. uniform dull grey-green, 12. uniform light grey. Spots, when present, varying in size and shape,

Figure 2. *N. dayi*, Atherton Tablelands, NEQ.

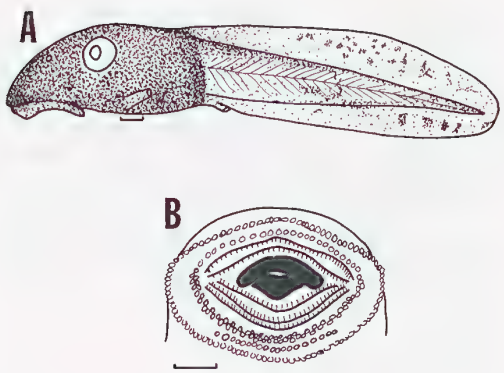

Figure 3. Tadpole of *N. dayi*. **A,** Lateral view. **B,** Mouthparts.

often having appearance of lichen. Although considerable intrapopulation variation exists, there may be a north-south cline in ground colour of dorsum, from predominantly creamish or grey in the north to dark brown in the south.

Life History. *N. dayi* breeds from October to April. Amplexus is axillary. In chorus, the advertising call of the breeding male is a drawn out "eeeeeeee" that inflects downwards at the end. This is given three to four times in succession. Solitary males can voice a short, sharp "ee" every five to six seconds, sometimes over long periods.

Large individually encapsulated unpigmented eggs are laid on rocks in water (some may be laid just above water line). Tadpole is torrent adapted with flattened body and head; strong muscular tail; tail tip round (Fig. 3A). Upper jaw strong, slightly curved inward and lower jaw V-shaped. Large suctorial mouth (Fig. 3B). Two complete rows of papillae surrounding outer margin of labia; inner row close to labial tooth row, posteriorly, with two layers of papillae. A short medial row of papillae between posterior inner and outer rows. Labial tooth rows: two complete upper and three lower rows; outer upper and lower labial rows weak. Anal opening median; spiracle on left, ventrolateral side of body. Sides and dorsal portions of body and head uniformly black; cream patch present between eyes and nostrils; tail cream with dark pigmentation dorsally on muscular tail.

The skewed sex ratio of frogs examined here (males 167 *vs* females 7) is not significant. This only indicates that the males have an advertising call and thus are much easier to locate and collect than the silent females.

Habitat. *Nyctimystes dayi* is essentially a frog of rainforest or rainforest margins throughout its range. In montane areas these frogs show a preference for fast-flowing, rocky streams although they also frequent slower watercourses where ample vegetation exists along the margins. At lower elevations, favoured situations include rocks soaks, narrow ephemeral streams and rock outcrops in larger watercourses. In many areas *N. dayi* is a conspicuous occupant of waterfalls and torrents along with tree-frogs of the *Litoria nannotis* complex.

Resting and calling males may be located on rocks and boulders both within the water and along the water's edge, low stream-side vegetation or overhanging branches. Non-amplexing females have been found on large mossy boulders and tall vegetation surrounding those watercourses where males were calling.

Distribution. In rainforests from the Bloomfield area, near Cooktown, south to Paluma, north to Townsville.

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References

Andersson, L.G., 1916. Results of Dr. E. Mjoberg's Swedish scientific expeditions to Australia, 1910—1913. ix. Batrachians from Queensland. Konglige Svenska Vetenskaps-Akademiens Handlingar (new series) 52(9): 1—20, pl. 1.

Barker, J. & G. Grigg, 1977. A field guide to Australian frogs. Rigby, Adelaide, pp. 229.

Cogger, H.G., 1975. Reptiles and Amphibians of Australia. 1st edition. Reed, Sydney, pp. 584.

_____ 1983. Reptiles and Amphibians of Australia. 3rd edition. Reed, Sydney, pp. 660.

Cogger, H.G., E.E. Cameron & H.M. Cogger, 1983. Zoological Catalogue of Australia Vol. 1. Amphibia and Reptilia. Australian Government Publishing Service, Canberra, pp. vi + 313.

Copland, S.J., 1957. Australian tree frogs of the genus *Hyla*. Proceedings of the Linnaean Society of New South Wales 82(1): 9—108.

Duellman, W.E., 1977. Liste der rezenten Amphibien und Reptilien: Hylidae, Centrolenidae, Pseudidae. Das Tierreich 95: 1—225.

_____ 1985. Hylidae. p. 110—203. **In** 'Amphibian species of the world' (ed D.R. Frost). Allen Press and Association of Systematics Collections, Kansas, pp. v + 732.

Günther, A., 1897. Description of new species of lizards and of a tree-frog from north-eastern Queensland. Novitates Zoologicae 4(3): 403—406, pls 11, 12.

Ingram, G.J. & J. Covacevich, J., 1981. Frog and reptile type specimens in the Queensland Museum, with a checklist of frogs and reptiles in Queensland. Memoirs of the Queensland Museum 20(2): 291—306.

Liem, D.S., 1974. A review of the *Litoria nannotis* species group, and a description of a new species of *Litoria* from northern Queensland, Australia (Anura: Hylidae). Memoirs of the Queensland Museum 17(1): 151—168, pls 3, 4.

Loveridge, A., 1935. Australian Amphibia in the Museum of Comparative Zoology, Cambridge, Massachusetts. Bulletin of the Museum of Comparative Zoology, Harvard 78(1): 1—62, pl. 1.

Schiøtz, A., 1967. The treefrogs (Rhacophoridae) of West Africa. Spolia Zoologica Musei Hauniensis 25: 1—346.

Tyler, M.J., 1964. Two new species of Australian frogs of the hylid genus *Nyctimystes*. Transactions of the Royal Society of South Australia 88: 111—114, pl. 1.

_____ 1968. An additional species of the hylid from genus *Nyctimystes* with notes on *Hyla dayi* Günther. Arkiv for Zoologi 20(22): 501—504.

_____ 1976. Frogs. Collins, Sydney, pp 256.

Tyler, M.J. & M. Davies, 1978. Species groups within the Australopapuan hylid frog genus *Litoria*. Australian Journal of Zoology, Supplementary Series No. 63, pp 47.

_____ 1979. Redefinition and evolutionary origin of the Australopapuan hylid frog genus *Nyctimystes* Stejneger. Australian Journal of Zoology 27(5): 755—772.

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Australian species of *Nerocila* Leach, 1818, and *Crenolia* n. gen. (Isopoda: Cymothoidae), crustacean parasites of marine fishes. ..... NIEL L. BRUCE 355

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The Functional Morphology of *Neotrigonia margaritacea* (Bivalvia: Trigoniacea), with a Discussion of Phylogenetic Affinities

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ABSTRACT. *Neotrigonia margaritacea* is one of six living Australian species of the Trigoniacea, an otherwise extinct group of Mesozoic 'cockles' which dominated shallow inshore seas worldwide. The Trigoniacea have usually been grouped with the freshwater Unionacea, each within its own order, in the sub-class Palaeoheterodonta. This taxonomic decision is largely based on hinge and shell structure, but other morphological evidence does not support such a contention, *Neotrigonia* being characterised by a lack of mantle fusion and possession of 'filibranch' ctenidia, the Unionacea by well developed siphons and 'eulamellibranch' ctenidia. Such morphological discrepancies sustain lively debate in the literature, but seem to have been resolved when the ciliary pathways on the ctenidia of both groups were described to be uniquely similar.

This study re-examines living *N. margaritacea* and investigates the histology of the ctenidia in particular, and concludes that in terms of structure and ciliary pathways, *Neotrigonia* is unique, and that its affiliations lie not with eulamellibranch bivalves but with the filibranch bivalves of the Pteriomorphia.

The myophorid origin of the Trigoniacea is undisputed, as is the widely held view that the group is terminal, i.e. it has not given rise to other bivalve lineages. It is noted, moreover, that some palaeontologists regard the Palaeoheterodonta as an artificial assemblage and the conclusion of this study supports the view that the Trigoniacea and Unionacea are not closely related. I believe the Trigoniacea to represent another line of pteriomorph evolution: perhaps sharing some remote palaeotaxodont ancestor with the Unionacea, but in no greater sense than that the same ancestors are believed to be those of probably all living bivalve groups.

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The extant Trigoniacea are the living remnants of a once diverse and populous group of Mesozoic bivalves that were widely distributed in shallow seas throughout the world, and with a centre of distribution in the Tethyan realm (Stanley, 1977). Today, they survive only in the waters of the south-west Pacific and around Australia (Fleming, 1964). Six extant species are recognised (McMichael, 1956; Habe, 1985), all belonging to *Neotrigonia*. A systematic revision of the Caenozoic Trigoniidae by Darragh (1986) suggests that *Neotrigonia* evolved from *Eotrigonia* in the Oligocene or early Miocene while *Eotrigonia* evolved from *Trigonia* s.s. in the late Cretaceous or early Tertiary. A visit to southern Australia under the auspices of the Association of Commonwealth Universities Senior Travelling Fellowship Scheme allowed examination of *N. margaritacea* (Lamarck, 1804). Because they were the most diverse and conspicuous shallow-burrowing component of near-shore marine assemblages in the Mesozoic, the Trigoniacea have received much attention from past (e.g., Lycett, 1879) and contemporary palaeontologists, e.g., Cox (1952), Fleming (1964), Newell & Boyd (1975) and Stanley

(1977; 1978). The latter author has comprehensively described the adaptive morphology of the group and its evolution.

The trigoniid shell is well known (Cox, 1952; McMichael, 1956; Taylor *et al.*, 1969; 1973; Newell & Boyd, 1975; Stanley, 1977; 1978), perhaps being the most studied of all bivalves. A wide variety of other authors, e.g., Ridewood (1903), Pelseneer (1911), Atkins (1938), White (1942), Purchon (1957), Gould (1969), Gould & Jones (1974) and Tevesz (1975), have described many aspects of tissue morphology summarised by Boss (1982), although as far as I can discover only Tevesz (1975) appears to have investigated living individuals. For reasons which will later become obvious it was decided to reinvestigate the anatomy of *Neotrigonia.*

Palaeontologists have held long debates over the Trigoniacea (Trigonioidea) and today the order is linked with the extant Unionoida (Unionacea) and the extinct Modiomorphoidea in the Palaeoheterodonta (Newell, 1969). The reasons for linkage with the Unionacea have a long, tortuous, history.

The Schizodontida, as originally defined by Steinmann (1903), included only the Trigoniacea but was extended by Neumayr (1884; 1889) to include the Unionacea (Naiadida) on the common basis of a nacreous shell, striated, schizodont hinge teeth and an unfused mantle margin. Douville (1912), however, pointed out that the similarity between these two groups is delusive, for the trigoniid tooth is not originally double as in the Unionacea, but is formed by division of a primitively simple tooth. Douville derived the Trigoniidae from the Preheterodonta by way of the Myophoridae, and most modern authors accept this, e.g., Cox (1952; 1969), Newell (1969), Newell & Boyd (1975) and Stanley (1977; 1978). The Trigoniacea are considered to be a terminal group (Douville, 1912).

The evidence of shell structure and mineralogy (Taylor *et al.*, 1969; 1973) and dentition sustain the view of linkage between the Trigoniidae and Unionacea, prompting Morris (1978, p. 268) to state that "the Unionacea are the result of separate invasions by Trigoniaceans of the non-marine habit", and Gould & Jones (1974, p. 5) to state that "The freshwater unionids are the closest living relatives of trigoniids".

Students of anatomy however, have found little evidence in support of this view. Most important evidence comes from studies of the ctenidia. On the basis of ctenidial structure, Ridewood (1903) placed the Trigoniacea in his order Eleutherorhabda (Sub-order Mytilacea), Pelseneer (1911) placed them in his order Filibranchia (Sub-order Arcacea) while Atkins (1938, p. 396) concluded that the arrangements of the ciliary tracts in the Naiadacea and Trigoniidae are "entirely different" prompting her to place the Trigoniidae in her order Filibranchia. Notwithstanding the above evidence, however, Tevesz (1975) concluded that the Trigoniacea had a gill ciliation of type D (Atkins, 1937b), hitherto believed to be uniquely possessed by the Unionacea. Such an observation seems to end the argument: the Trigoniacea and Unionacea now being linked by similarities in shell and tissue morphology and function.

This study, however, re-examines the morphology of *Neotrigonia margaritacea,* disputes the conclusion of Tevesz (1975), re-opens the discussion on trigoniid affinity with the Unionacea and comes to a number of conclusions of its own.

Materials and Methods.

Living specimens of *Neotrigonia margaritacea* were studied, during January 1985, at the Marine Science Laboratories, Queenscliff, Victoria, of the Department of Conservation, Forests and Lands of the Victorian Government, Australia. Ciliary currents were elucidated using Carmine in sea water. Subsequently I received a collection of preserved specimens of the same species dredged from 10 m in the North arm of Western Port Bay, Victoria, during 13—14 Feb 1985. These specimens, preserved in vapour-suppressed, neutral formalin, were subsequently dissected and two of them, following removal from the shell, were serially sectioned transversely and sagittally at 6 μm.

Additionally, pieces of ctenidia were removed from other specimens and sectioned transversely at 4 μm. Alternate slides of the whole animals were stained in either Ehlich's haematoxylin and eosin or Massons' trichrome. Sections of the ctenidia were additionally stained in Heidenhain's haematoxylin and light green. Specimens of *Mytilus edulis* from Great Britain, and *Barbatia virescens* and *Anodonta woodiana* from Hong Kong, have been sectioned and stained as above for comparison of ctenidial ciliation.

Abbreviations used in the figures are listed below.

A-Anus, AA-Anterior adductor muscle (or scar), APP-Anterior pedal protractor muscle (or scar), APR-Anterior pedal retractor muscle (or scar), AS-Anterior socket, AU-Auricle, C-Cilia, CA-Ctenidial axis, CD-Ciliated disc, CFC-Coarse frontal cilia, CM-Circular muscle, CR-'Chitinous' rod, CT-Ctenidium, DOG-Distal oral groove, ELFC-Eulaterofrontal cilia, E'S'-Exhalant 'siphon', FC-Frontal cilia, FFC-Fine frontal cilia, FG-Food groove, F(H)-'Heel' of foot, F(T)-'Toe' of foot, GA-Gonadial aperture, GR-Groove, H-Haemocoel, HE-Heart, ID-Inner demibranch, ILP-Inner labial palp, IMF-Inner mantle fold, I'S'-Inhalant 'siphon', K-Kidney, L-Ligament, LC-Lateral cilia, LFC-Long frontal cilia, LFP-Lateral foot papillae, LIM-lips of mouth, LM-Longitudinal muscle, LP-Labial palp, MC-Mucous cell, MFP-Median foot papillae, MLFC-Microlaterofrontal cilia, MM-Mantle margin, MF-Middle mantle fold, OD-Outer demibranch,

OM-Oblique muscle, OMF-Outer mantle fold, P-Pericardium, PA-Posterior adductor muscle (or scar), PAB-Posterior aortic bulb, Palid-Point of attachment of ascending lammella of inner demibranch to visceral mass, PE-Periostracum, PEM-Pedal elevator muscle (or scar), PG-Pericardial gland, PL-Pallial line, PLFC-Prolaterofrontal cilia, PP-Papilla, PPR-Posterior pedal retractor muscle (or scar), PR-Pallial ridge, PRM-Pallial retractor muscle, PS-Posterior socket, R-Rectum, RA-Renal aperture, RPA-Renopericardial aperture, TM-Transverse muscle fibres, V-Ventricle, VM-Visceral mass

FUNCTIONAL MORPHOLOGY

Shell. There are already many substantial descriptions of fossil and Recent trigoniids (Lycett, 1879; Fleming, 1964; Newell & Boyd, 1975) and interpretations of shell morphology (Stanley, 1977; 1978). It is, however, appropriate to briefly review important features. The shell (Fig. 1) is cockle-shaped with a small external, parivincular, opisthodetic ligament (L). As noted by Stanley (1977; 1978), the trigoniid shell is unusual in that the umbones are orthogyrous — an uncommon feature among other burrowing bivalves where typically the beaks are prosogyrous. The external surface of the shell is radially sculptured with pronounced pustulose ribs forming an interlocking, scalloped margin. Taylor *et al.* (1969) have shown the shell to be aragonitic and to comprise three layers. The outer is prismatic, the middle and inner layers of lenticular and sheet nacre respectively. The hinge teeth are relatively enormous and comprise, in the right valve, two diverging, blade-like teeth that interlock with two deep and narrow sockets (AS;PS) in the left valve. The articulating surfaces of both teeth and sockets possess well developed transverse ridges and grooves (Newell & Boyd, 1975) that serve to sustain valve alignment during those times when the valves gape widely, as during leaping (Stanley, 1977; 1978). This is because the angle of gape required for burrowing (or leaping) greatly exceeds that observed for most other bivalves (Stanley, 1977; 1978). The anterior tooth and socket are each supported by a strong buttress. The pallial line (PL) is entire, simple and deeply recessed from the valve margin. The positions and arrangements of major muscle scars will be described later. Smith (1983) has shown that representatives of the Margaritiferidae, alone among the Unionacea, possess small mantle-shell attachment scars. These also occur in members of the Trigoniacea, strengthening arguments for a link between the Unionida and Trigonioida.

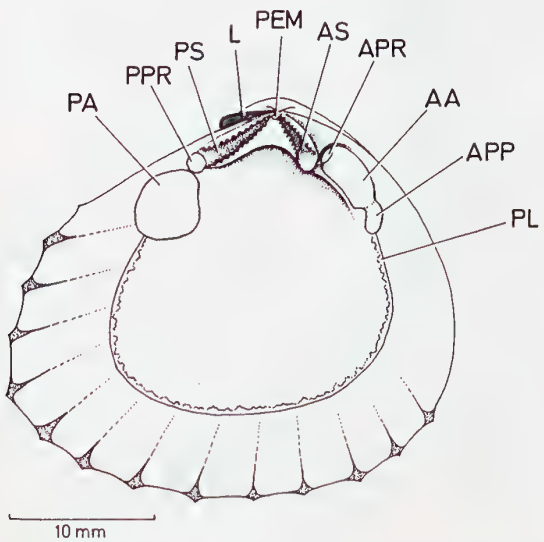

Fig. 1. *Neotrigonia margaritacea.* Internal view of left shell valve. (For abbreviations see 'Materials and Methods').

Mantle and siphons. The mantle is relatively featureless and Figure 2 shows the ventral mantle margin in transverse section. It is remarkably simple with the usual three folds (Yonge, 1957; 1982); inner (IMF), middle (MMF) and outer (OMF) — all small and of uncomplicated structure. There is an extensive haemocoel (H) between mantle epithelia. From the periostracal groove arises a thin (8 μm), single-layered periostracum (PE). The inner and middle folds possess small, presumably sensory, papillae (PP) that extend all the way around the unfused anterior, ventral and posterior margins of the mantle. The papillae of the middle fold are uniformly small and evenly distributed. Anteriorly, however, the papillae of the inner fold are modified to define two 'siphons', functionally but not morphologically delineated by pallial fusions (Fig. 3). Anteroventrally, the inner fold, demarcating the inhalant 'siphon' (I'S'), possesses three outwardly arranged rows of tentacles. In an adult specimen (i.e. of shell length 25—35 mm), there are usually seven large, ramose, tentacles. These are interspersed by a further array of eight smaller, but still ramose tentacles. Each tentacle alternates with the third, outermost, array of small papillae. This inhalant 'siphon' is functionally separated from the exhalant (E'S') by a pallial ridge (PR) (Gould & Jones, 1974). These authors conclude that when left and right mantle edges are applied to each other, the pallial ridges will be apposed, producing a firm division between inhalant and exhalant waters. The ridges are fed by branches from the posterior aorta and are probably inflated hydraulically by blood from the circulatory system — perhaps that contained within the pallial haemocoels described above. The exhalant 'siphon' is delineated by a dense array of smaller and larger papillae which extend along the anterodorsal edge of the inner folds, but also densely cover the outer surface of this fold. Anterior enlargement of the pallial retractor muscles

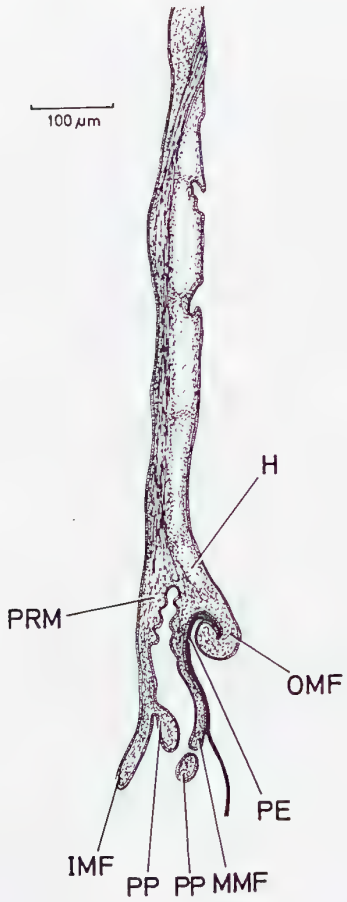

Fig. 2. *Neotrigonia margaritacea.* Transverse section through right mantle margin. (For abbreviations see 'Materials and Methods').

creates a siphonal musculature that is responsible for retracting the siphons, by inverting them, prior to valve closure.

Musculature and foot. There are anterior and posterior adductor muscles (Figs 1 and 4, AA; PA), the latter more rounded and somewhat larger than the former, which is dorsoventrally elongate. Both are located high up on the shell and internal to each is a large pedal retractor muscle (APR; PPR). The posterior is located anterodorsally to the posterior adductor; the anterior dorsally to the anterior adductor, being inserted on the anterior face of the buttress supporting the anterior hinge tooth or socket. In addition to these usual pedal muscles, there are two others. Paired anterior pedal protractor muscles (APP) are located ventral to the anterior adductor and send branches into the foot to pull it forwards. Paired pedal elevator muscles (PEM) arise from just beneath the umbones and extend into the posterior regions of the visceral mass to pull it upwards and backwards. These muscles were commented upon by Fleming (1964) and are characteristic of all Recent and extinct trigoniaceans. Fleming believed left and right pedal elevator muscles to be unequal, the left larger than the right. This, however, is not so, the illusion being created by the fact that the left muscle is more deeply inserted into the umbones behind the hinge teeth sockets of the left valve, whereas the insertion of the right is less deeply impressed by virtue of it being between the hinge teeth of the right valve.

The visceral mass and foot of *Neotrigonia* are most unusual, comprising a muscular, column-like, visceral mass which terminally expands into an anchor-like foot comprising a posterior 'heel' (Figs 4 and 5, F(H)) and an anterior 'toe' (F(T)). The anterior portion of the foot retracts closely against the visceral mass, the dorsal edge of the 'toe' fitting into a groove

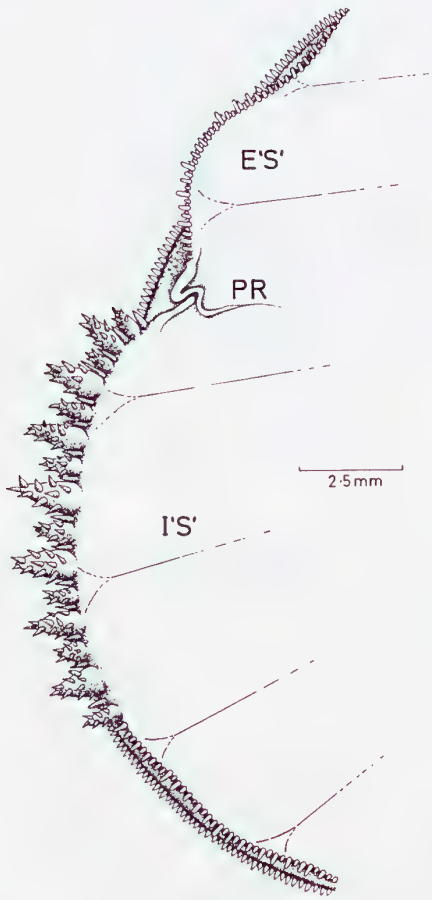

Fig. 3. *Neotrigonia margaritacea.* Left posterior mantle margin, showing inhalant and exhalant 'siphons'. (For abbreviations see 'Materials and Methods').

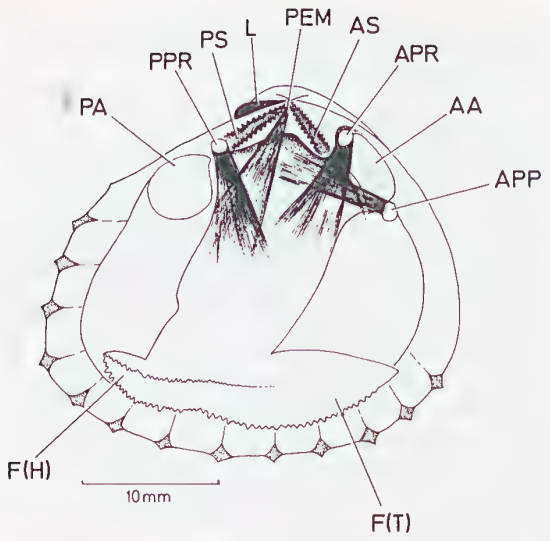

Fig. 4. *Neotrigonia margaritacea.* Visceral mass and foot, with musculature, as seen from right side. (For abbreviations see 'Materials and Methods').

(GR) on the anterior face of the visceral mass. From the posterior to the anterior, the foot is medially lined by a series of papillae (Fig. 6, MFP) which are possibly sensory. Similarly, from the posterior end a second series of lateral papillae (LFP) extend around each side of the foot to about halfway along its length. Apparently during leaping, the sole of the foot can be flattened to form a sucker-like disc, adhesion being aided by secretions from glands in the sole of the foot (Gould, 1969). Tevesz (1975) has described the burrowing sequence of *N. gemma.* Gould (1969) has described from the foot of *N. margaritacea* a small byssal apparatus which is functionless in the adult and represents the remnant of a juvenile organ, reduced by allometry.

The form of the foot in transverse section (Fig. 5) is trefoil, the medial (MFP) and lateral (LFP) series of papillae, creating this unusual shape. The musculature of the foot is complex and comprises a number of layers. Beneath the outer epithelium is a thick layer of longitudinal muscles (LM). Beneath is a layer of oblique muscles (OM) surrounding an extensive layer of circular muscles (CM) that sends fibres into the lateral and medial papillate ridges of the foot's sole. The central region of the foot, bounded by the circular muscles, is occupied by longitudinal muscles (LM) enclosing a capacious haemocoel (H). The two sides of the foot, but especially the central region of longitudinal muscles, are cross-connected by transverse muscle fibres (TM).

Such complexity of structure and, especially musculature, clearly point to an active, burrowing life style with the added capacity for leaping, possibly for defensive purposes.

Ciliary currents of visceral mass and mantle. The visceral mass is richly endowed with cilia that subserve a cleansing function (Fig. 6). Dorsally, ciliary currents sweep material forwards, but such material eventually passes downwards and then is turned posteriorly to contribute to a major rejectory tract on that region dividing visceral mass from foot. Material entering this tract passes posteriorly and eventually falls off, onto the mantle, from a point just above the 'heel' of the foot. The rejection tract is also contributed to by a few ciliary currents on the foot, but this organ is typically free of ciliary activity.

The ciliary currents of the mantle (Fig. 7) approximate those of the visceral mass. Dorsally, the currents sweep forwards but eventually material passes downwards and then is turned posteriorly to contribute to a major rejectory tract on each mantle lobe. Extending along the inner edges of the ventral mantle margins such tracts also receive material from the rejection tracts on the visceral mass. The accumulated waste material flows towards the inhalant siphon in these two streams and is expelled eventually as a pseudofaecal bolus from the ventral borders of the inhalant 'siphon'.

Ctenidia and currents. One of the most remarkable, indeed bafflingly odd, features of *Neotrigonia* are the 'filibranch' ctenidia (Ridewood, 1903; Pelseneer, 1911; Atkins, 1938). Most precisely, this refers to the fact that the individual filaments are not united ventrally with their neighbours except by opposing ciliary discs on the lateral bases of the filaments. The ctenidium is therefore filibranch, homorhabdic and

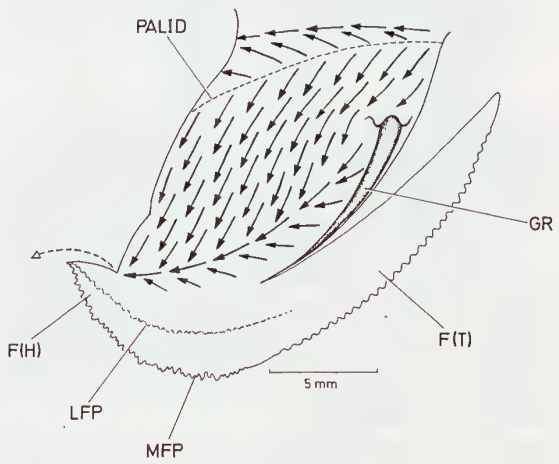

Fig. 5. *Neotrigonia margaritacea.* Transverse section through foot, showing the extensive musculature. (For abbreviations see 'Materials and Methods').

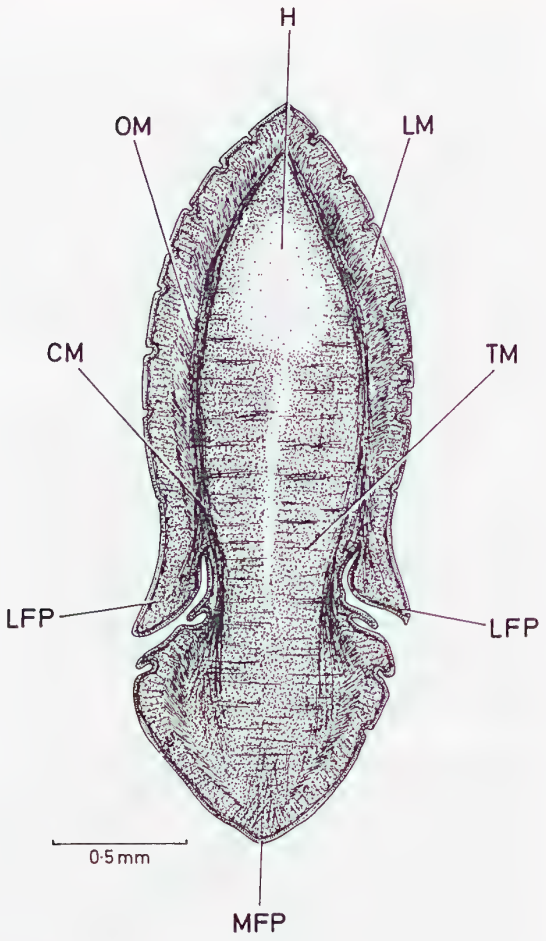

Fig. 6. *Neotrigonia margaritacea.* Visceral mass and foot, as seen from the right side and showing ciliary currents. (For abbreviations see 'Materials and Methods').

nonplicate. Each ctenidium comprises two demibranchs (Fig. 8), the outer (OD) of which is dorsoventrally shorter than the inner (ID). As in some other bivalve groups, e.g. the Arcacea, Anomiacea and Pectinacea, the ctenidia extend beyond the posterior border of the visceral mass, so that the posterior ends are free and broadly separate, with the pallial ridge separating supra- from infra-branchial chambers. The outer demibranchs are also slightly shorter anteroposteriorly than the inner so that, as will be explained, only the inner demibranchs extend into the distal oral grooves.

The upper margins of the ascending lamellae of the inner and outer demibranchs are only weakly attached to the visceral mass and mantle respectively (Fig. 9). This is the result of a delicate union of opposing cilia (C), 4—5 μm long. Such a situation is seen elsewhere only in members of the Palaeotaxodonta, Pteriomorphia (Grobben, 1900; Atkins, 1937a) the Anomalodesmata (Morton, 1985) and *Ensis* (Atkins, 1937c).

The structure of an individual ctenidial filament, first described by Ridewood (1903) and Atkins (1938), is illustrated in Figure 10. Its structure is unique in the Bivalvia with the frontal ciliation largely separated from the remainder of the filament. Closest structural similarities are with the palaeotaxodont *Nuculana* where "disposition of the cilia approaches the arrangement .... in *Trigonia* alone among Lamellibranchs" (Atkins, 1937a, p. 194). Thus, apically, the filament comprises in transverse section a rounded 'head' attached by a 'stalk' to the remainder. On the 'head' are three ciliary tracts: an apical series of cells with short (4 μm) coarse frontal cilia (CFC), flanked on either side by long (8 μm) frontal cilia (LFC). According to Atkins (1938), the 'stalk' too is ciliated with short (2—3 μm), fine frontal cilia (FFC). I, however, have had difficulty in deciding whether or not such structures are indeed cilia or microvilli, especially since the cells they arise from are not columnar, but comprise a flattened squamous epithelium. The central section of the filament comprises those cells concerned with filtration. The lateral cilia (LC) are long (12 μm) and create the flow of water between filaments. Apically from these are the cells bearing the eulaterofrontal cilia (ELFC) which are long (18 μm), with pronounced ciliary rootlets. Separating these two cell types is a mucous cell (MC). The basal component of the filament comprises cells which bear the cilia of the ciliated discs (CD). The filament is supported by distinctive 'chitinous' rods (CR), but it is significant

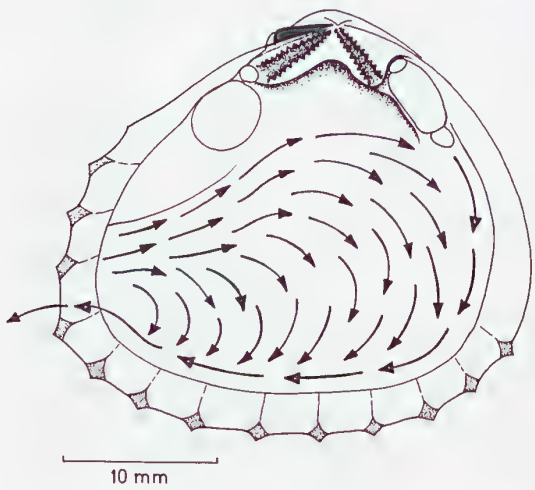

Fig. 7. *Neotrigonia margaritacea.* Mantle of left valve, showing ciliary currents. (For abbreviations see 'Materials and Methods').

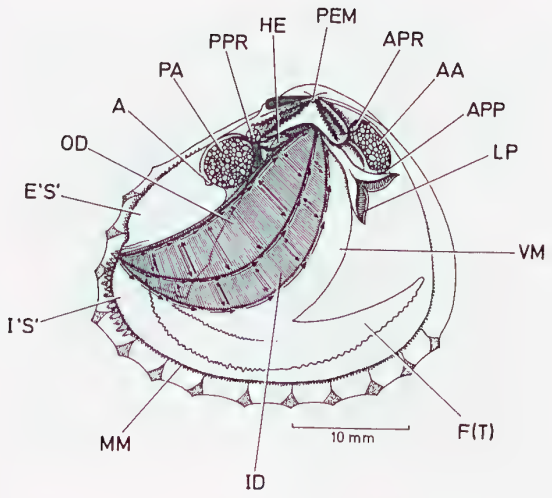

Fig. 8. *Neotrigonia margaritacea.* Internal view of organs of mantle cavity, as seen from right side and showing ciliary currents of right ctenidium. (For abbreviations see 'Materials and Methods').

that the major structural enlargement of the rods is basal, as in the Pteriomorphia (Fig. 16A and B) but not eulamellibranchs (Fig. 16C), and thus only flexibily support the central stalk and apical components of each filament. Atkins (1938) reports that the chitinous rods of *Neotrigonia* are calcified basally, as elsewhere seen only in species of the Unionacea (Ridewood, 1903). I can not differentiate such a structural difference between the 'chitinous' rods of *Neotrigonia* and other bivalves. The haemocoel that the filament encloses is richly endowed with leucocytes, and the chitinous rods are cross-connected by transverse fibres.

Importantly, Tevesz (1975) considers the ctenidial ciliation of *Neotrigonia* to be of Type D, as seen elsewhere only in the Unionacea (Atkins, 1937b). This is not so. Particles placed on the ctenidial surfaces move upwards and downwards, this being the differential function of the two types of frontal cilia on the apical 'head' of the filament. Oralward acceptance tracts are located in the ventral marginal grooves of both demibranchs, the ctenidial axis, and in the junctions of the ascending lamellae of the inner and outer demibranchs with the visceral mass and the mantle respectively. The gill ciliation (Fig. 11) is thus of Type B(1b) (ordinary filaments) and thus typical of most 'pseudolamellibranch' families, e.g. Pteriidae, Pectinidae, Limidae and Ostreidae. A similar condition defined as C(1a) (ordinary filaments) is seen in the Solenidae. In the majority of the above bivalves, however, the ctenidium is deeply plicate and up or down transfer of particles on the surface of the ctendium is the responsibility of different filaments. Only in the Arcacea and Anomiacea does the homorhabdic filament head possess differentiated ciliary tracts of coarse and fine frontal cilia resulting in the ctenidium fulfilling a particle sorting role. In these bivalves, however, the ventral marginal grooves pass material posteriorly for rejection as pseudofaeces. This type of ctenidium is defined as type B(1a) (Atkins, 1937b) and, but for the posteriorly directed ventral rejection tracts, most closely approximates the situation seen in *Neotrigonia.* Reversal of these ventral tracts, orally, would produce a ctenidium with a structure, ciliation and sorting function very reminiscent of *Neotrigonia.* Thus in terms of frontal ciliation, the ctenidium of *Neotrigonia* is most like the Arcacea and Anomiacea, but in terms of ciliary currents it is most like the Pseudolamellibranchia. I believe *Neotrigonia* to represent a unique condition, possibly intermediate between these groups of bivalves.

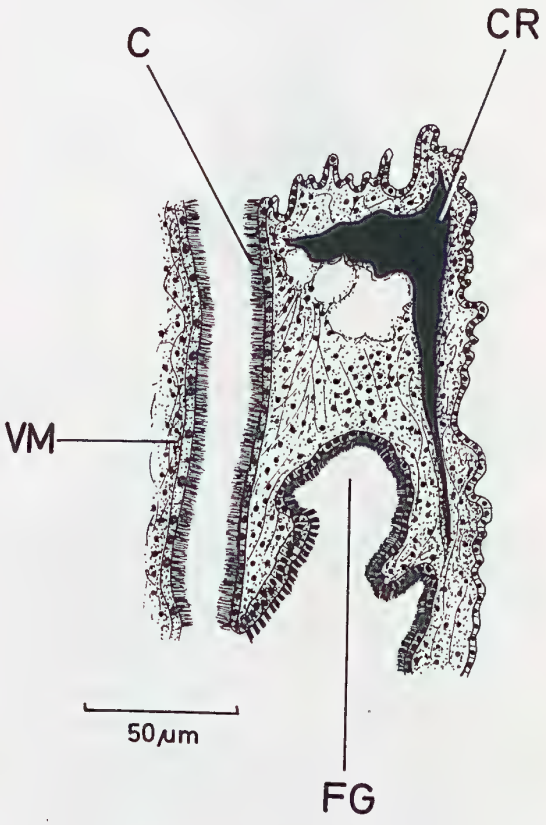

Fig. 9. *Neotrigonia margaritacea.* Transverse section through dorsal edge of right ascending lamella of inner demibranch with visceral mass showing ciliary union. (For abbreviations see 'Materials and Methods').

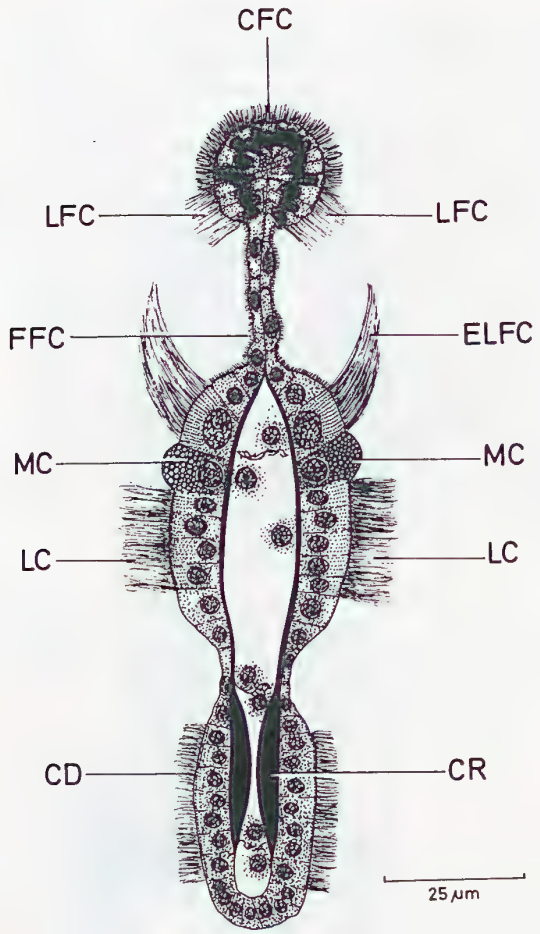

Fig. 10. *Neotrigonia margaritacea.* Transverse section through single ctenidial filament, showing arrangement of cilia. (For abbreviations see 'Materials and Methods').

Labial palps. Figure 12 is an enlarged view of the anterior end of the right ctenidium and associated labial palps. The anteriormost filaments of the inner demibranchs (ID) only extend into the distal oral groove (DOG) so that material arriving at the ctenidial terminus in the food grooves of the outer demibranch (OD) must pass onto the inner demibranch, if only briefly, before proceeding further. Such a ctenidial-labial palp junction is of Category 3, possessed by a number of other bivalve groups including members of the Pteriomorphia, Palaeoheterodonta (i.e. Unionacea), Heterodonta and Anomalodesmata (Stasek, 1963), while the forshortened outer demibranch is characteristic of the Mytilacea (Pteriomorphia) (Morton, 1987).

The distal oral grooves are long, and probably the ventral marginal food grooves of the inner demibranchs fit into them in life so that material is more effectively passed to the labial palps. The palps (ILP, OLP) are relatively small and extend as two triangular extensions of the distal oral grooves and lips of the mouth (LIM) on each side of the visceral mass just beneath the anterior adductor (AA) and anterior pedal protractor muscles (APP). Material passes down the distal oral groove and then passes onto the fused distal edges of the palps and thence between their inner faces. These comprise a series of ridges and grooves (Fig. 13) extending at right angles to the proximal oral grooves. Material reaching the inner faces either quickly passes over the crests of the ridges (if it is small and light enough) into the proximal oral groove and is accepted, or passes into the grooves between palp crests where it is subjected to a number of resorting currents and is thus either

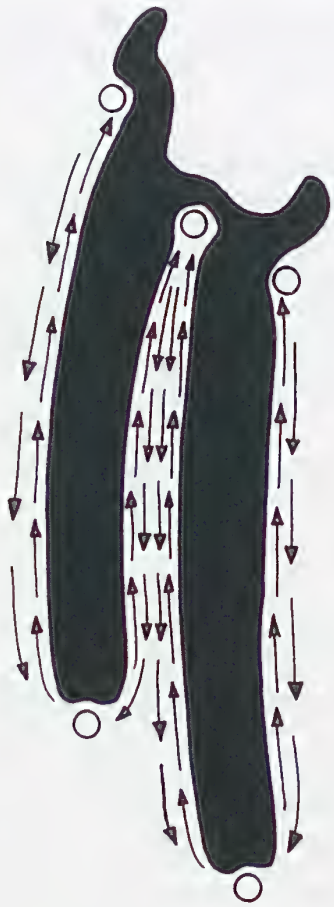

Fig. 11. *Neotrigonia margaritacea.* Diagrammatic transverse section through left ctenidium showing arrangement of ciliary currents on each lamella and the five oral food grooves (O).

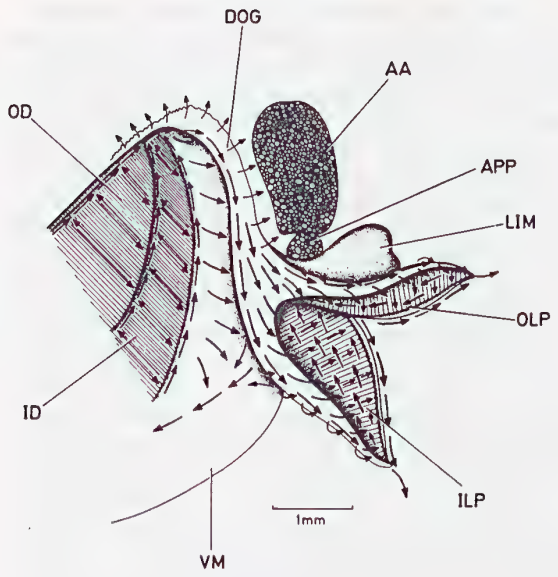

Fig. 12. *Neotrigonia margaritacea.* Detail of anterior end of ctenidium on right side and labial palps, with ciliary currents. (For abbreviations see 'Materials and Methods').

returned to the crests of the ridges or is rejected and falls into the depths of the grooves. The latter material is passed to the edge of each palp and is then transferred to the palp tip where it is rejected and becomes incorporated into the cleansing system of the visceral mass and mantle to be ultimately rejected as pseudofaeces. The palp ciliation is thus of the typical bivalve form, sustaining an important role in the sorting of material collected by the ctenidia.

Alimentary canal. The course of the alimentary tract in *Neotrigonia* has been illustrated by Gould (1969, Fig. 1), while Purchon (1957) has described the structure of the stomach and assigned it to Type 4, also possessed by representatives of the Pteriomorphia, Palaeoheterodonta (i.e. Unionacea), Heterodonta and Anomalodesmata (Purchon, 1957; 1958; 1960). Of importance are the facts that (1) the style sac and mid gut are conjoined, (2) the rectum is traversed by the ventricle of the heart, and (3) the stomach is characterised by the concentration of ducts to the digestive diverticula into three large embayments, extreme reduction of food-sorting caecum, the absence of a well developed tongue of the major typhlosole, the great development of the dorsal hood and its contained sorting areas, and the great development of the 'posterior sorting area' on the right wall of the stomach. On the basis of these structural features, Purchon (1957) considered the stomach of *Neotrigonia* to most resemble those of representatives of the Limidae, Pectinidae and Anomiidae (Pteriomorphia).

Organs of the pericardium. The structure of the pericardium of *Neotrigonia* has been briefly described by White (1942). The pericardium (Fig. 14, P) is located just beneath the posterior hinge tooth and socket. The heart comprises a single ventricle (V) with an anterior and a more pronounced, posterior aortic bulb (PAB) and is also traversed by the rectum (R). The lateral auricles (AU) are triangular and their walls and, to a lesser extent, those of the pericardium possess elements of the pericardial gland (PG). From the posteroventral margin of the pericardial cavity arise the paired renopericardial apertures (RPA) leading into the paired, light brown kidneys (K). The kidneys extend beyond the confines of the visceral mass within and above the ctenidial axis (CA). Pelseneer (1891) and White (1942) consider the kidney of *Neotrigonia* to most closely resemble that of the Arcidae.

From each kidney (Fig. 15, K) arises a renal aperture (RA) that discharges ventrally into the suprabranchial component of the mantle cavity. Just anterior to each of these is a gonadial aperture (GA) leading into the dorsally situated and paired gonads. *Neotrigonia* is dioecious.

Discussion

The Trigonioida, a group of Mesozoic 'cockles',

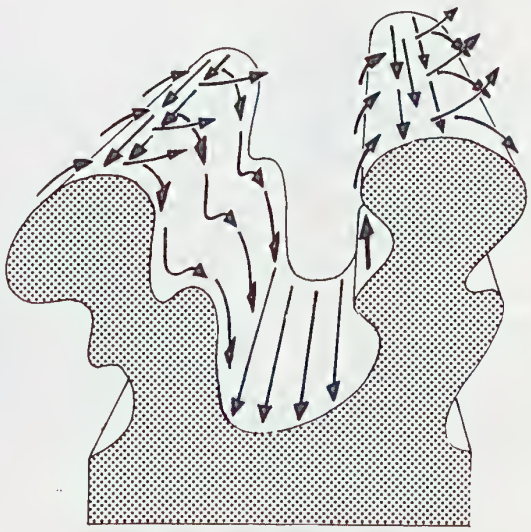

Fig. 13. *Neotrigonia margaritacea.* Diagrammatic transverse section through two palp ridges showing arrangement of ciliary tracts on various areas of their crests and grooves.

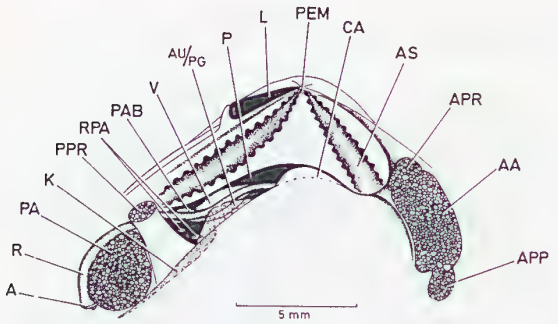

Fig. 14. *Neotrigonia margaritacea.* Detail of hinge region of the valve, showing structure of organs of pericardium. (For abbreviations see 'Materials and Methods').

survive today in Australian waters as living remnants of a once diverse and populous order and sustain lively debate in the literature. They have traditionally been located, along with the Unionoida and the extinct Modiomorphoida in the Palaeoheterodonta. Such conclusions, especially with regard to their affiliation with the Unionoida, arise because of the supposed common possession of schizodont hinge teeth (Cox, 1969), a similar shell mineralogy and microstructure (Taylor *et al.*, 1969; 1973), mantle-shell attachment scars (Smith, 1983) and similar gill ciliation (Tevesz, 1975). This relationship, especially in the light of this research, bears further discussion. First, it is worth quoting Cox (1969, p. 52) at length, with regard to the hinge teeth. "The term schizodont has little value. It was originally applied primarily to the type of dentition found in the family Trigoniidae, in which the median tooth of the left valve, one of a small number radiating from the beaks, is broad and bifid. This feature has no particular significance, as bifid teeth are found in many other groups, including many heterodonts. Forms belonging to the fresh-water superfamily Unionacea have been described as schizodont, as their dentition shows some similarity to that of the Trigoniacea, although not in this particular respect. The type of hinge found in these two superfamilies probably arose independently from the actinodont type." This argument strengthened the earlier views of Cox (1960) who thought that the Unionacea and Trigoniacea should be placed in separate orders, a view from which no student of the Trigoniacea has dissented. Newell (1969, p. 215) also believed that "The Palaeoheterodonta comprise(ing) the early actinodonts, unionaceans, and trigonaceans may be an artificial grouping". Newell concluded that the actinodonts, comprising the oldest known bivalves, may have given rise to the Pteriomorphia, Heterodonta and possibly other groups.

The second argument, that the Unionacea are more closely related to the Trigoniacea in comparison with other groups on the basis of shell mineralogy and microstructure (Taylor *et al.*, 1969; 1973), can also be questioned. These authors showed that such a shell structure is also possessed by the Anomalodesmata and, with slight variations in outer layer structure, i.e., aragonitic complex prisms or calcite simple prisms (instead of aragonitic simple prisms), by some superfamilies of the Palaeotaxodonta and Pteriomorphia respectively. Ben Mlih (1983), however, has re-examined shell structure in *Neotrigonia margaritacea* and shown that the outer layer comprises complex prisms, not simple as described for this species by Taylor *et al.* (1969). In such a case, shell structure is closest to the Palaeotaxodonta. The common possession by *Neotrigonia* and species of *Margaritifera* (Unionacea) of mantle-shell attachment scars has also been used to suggest common origins (Smith, 1983). Although the Margaritiferidae may be primitive (Smith, 1983), it is not known to what extent similar scars occur in older representatives of other phylogenies also. Third and finally, although most earlier authors (i.e. Ridewood, 1903; Pelseneer, 1911; Atkins, 1938) recognised that an important difference between the Trigoniacea and Unionacea was the filibranch and eulamellibranch ctenidia

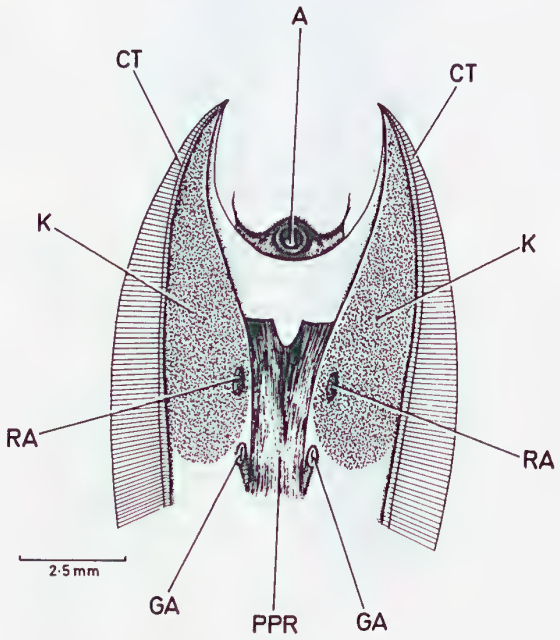

Fig. 15. *Neotrigonia margaritacea.* Ventral view of posterior ends of ctenidia, showing kidneys, anus and renal and gonadial apertures. (For abbreviations see 'Materials and Methods').

respectively, Tevesz (1975) concluded that both have a similar pattern of gill ciliation (Type D)(Atkins, 1937b). This study has shown that this is not true and that whereas ctenidial structure is most like that of *Nuculana* (Palaeotaxodonta) (Atkins, 1937a), the ctenidial currents most closely approximate type B(1b)I (characteristic of the Pteriomorphia) (Atkins, 1937b). This is not, however, because of heterorhabdy, as in many pteriomorphs, but rather because each filament has a frontal ciliation that effects sorting — a situation more reminiscent of other members of the Pteriomorphia (e.g., Arcacea and Anomiacea), albeit homorhabdic, macrociliobranch and non plicate — but nevertheless filibranch in general plan. The trigoniacean ctenidium is in fact unique in both structure and ciliation, but its affinities lie with 'filibranch' not 'eulamellibranch' grades or organization. Figure 16 compares filament structure in A, *Barbatia virescans* (Arcacea) B, *Mytilus edulis* (Mytilacea) and C, *Anodonta woodiana* (Unionacea) and from which (with comparison of Figure 10) it can be seen that *Neotrigonia* bears close similarities in terms of frontal ciliation with the Arcacea, but is macrociliobranch like *Mytilus*. The absence of inter-filamentar and inter-lamellar junctions, as in *Anodonta*, precludes close association with *Neotrigonia*, especially since all unions in the trigoniid are ciliary — features of the most primitive palaeotaxodont and pteriomorph ctenidia. In fact, Atkins (1938) thought the filament of *Neotrigonia* compared most clearly with that of *Nuculana minuta* (Palaeotaxodonta) (Atkins, 1938, p. 373, fig. 8), but to this author a more relevant comparison is with the situation in the Arcacea and Anomiacea (Type, B(1a)) but with the reversal, orally, of the currents of the ventral marginal grooves. Clearly these bivalves are reminiscent of primitive conditions in the Bivalvia, the ctenidia having a sorting function and unwanted particles being rejected from the ctenidia in the ventral marginal grooves. In all other bivalves, currents in these grooves are oral and it is clear that at some time an intermediate condition must have evolved. I believe *Neotrigonia* to be representative of such an evolutionary intermediate condition and forming a unique link between the more primitive ciliation of the Arcacea and Anomiacea and the remainder of the 'filibranch' bivalves. The importance of this, is that conditions in *Neotrigonia* are thus those which facilitated the enormous subsequent success of the modern suspension feeding Bivalvia in the Mesozoic and Caenozoic.

Importantly, Purchon (1978) has constructed a cladogram of bivalve relationships based on the multivariate analysis of nine character states. His results indicated affinity between the Trigoniacea,

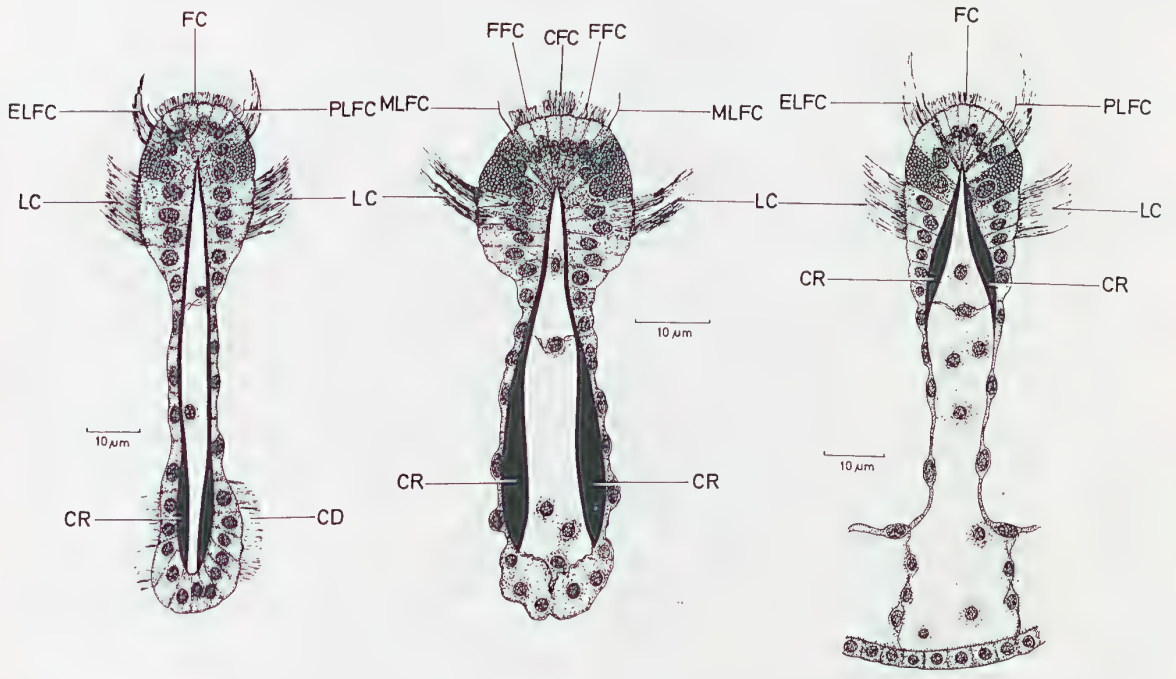

Fig. 16. Transverse section through gill filaments of **A**, *Mytilus edulis*; *B, Barbatia virescens* and **C**, *Anadonta woodiana*. A and C, from Hong Kong, B from Great Britain. These should be compared with Figure 10. (For abbreviations see 'Materials and Methods').

Unionacea, Lucinacea and Crassatellacea at about the 76 percentage similarity level. Despite this, Purchon (1978, p. 431) concluded that "the Unionacea and Trigoniacea should not be isolated in a subclass Palaeoheterodonta, but should be transferred into the subclass Heterodonta". Stanley (1977; 1978) has made a detailed study of the Trigoniacea and concluded that they arose from a schizodian grade ancestor (Schizodiidae) in the late Palaeozoic and radiated in the Mesozoic to produce a trigonian grade dentition via the intermediary of a myophorian grade dentition. The Trigoniacea therefore seem to represent a Mesozoic group of bivalves, related to the oldest bivalves and from which probably nearly all bivalve groups have subsequently arisen (Newell, 1969). Thus, the curious suite of morphological characters found in the Trigoniacea form a co-adaptive system that represents an alternative to the sets of characters found in other groups of burrowing bivalves (Stanley, 1977). Do the characters of *Neotrigonia* here further elucidated support this contention?

Table 1 compares *Neotrigonia* with other bivalve superfamilies on the basis of eight character states, with appropriate subcharacterisation. From this comparison it can be seen that it would be very difficult indeed to find a close living relation of *Neotrigonia*. The Trigoniacea seem to have affinities with representatives of virtually every bivalve order and if the term 'schizodont' is ignored, a close relationship with the Unionacea is not at all apparent. One wonders if the conclusions reached by Purchon (1978) would have been very different if the term 'schizodont' (a term considered delusive by Douville (1912)) had not been used in the analysis and if greater account was taken, instead, of ctenidial structure.

It is not suggested that the character states herein used all possess equal, if any, phylogenetic value. Indeed it is clear that althouth some are adaptive features (characteristic of the Trigoniacea when seen in concert (Stanley, 1977; 1978)), others are convergent and yet others simply 'bivalve' features. Thus, two adductor muscles are bivalve characters, the variation in size between groups being adaptive. Alternatively, the presence of pedal protractor muscles, but more importantly pedal elevator muscles, is an adaptive feature clearly indicative of an active foot, both for rapid burrowing and escape. This is amply exemplified by those bivalves which possess such features (e.g. the burrowing Heterodonta) which, with ventral mantle fusion, the formation of siphons and a eulamellibranch ctenidium, have greatly improved the efficiency of suspension feeding and permitted colonisation of the soft intertidal — a habitat from which the Trigoniacea, for converse reasons, were excluded (Stanley, 1968).

Generally, convergent features have been largely excluded from the analysis, there being little point in exposing similarities in overall shell form between the many 'cockle' groups (e.g. Arcacea and Cardiacea) and *Neotrigonia*, just as the triangular heteromyarian form has little significance in differentiating between those many epibyssate lineages that possess it.

Purchon (1960b) has argued that stomach structure has important phylogenetic meaning, but the similarities between that of *Neotrigonia* and a wide array of other bivalves (Table 1) suggest that structure, because the filtered material so obtained is most efficiently digested in a similar manner, may be highly adaptive too. Gill structure may also be adaptive, but nevertheless, grades of specialisation are well known (Atkins, 1938) and the clear relationship is between *Neotrigonia* and the Pteriomorphia (Table 1). Purchon (1978) confined his comparison of gill ciliation to macro- and microciliobranch conditions (Atkins, 1938). The evolution of eulaterofrontal cilia in the Bivalvia possibly has only limited phylogenetic value, being a highly adaptive character trait. Of much more value must be the combined character traits of the ctenidium, as discussed earlier.

Associated with simpler, filibranch, ctenidial ciliation is the lack of pallial fusions (Stanley, 1968) and this holds true for *Neotrigonia*, again with a clear relationship to the Pteriomorphia standing out.

The picture emerging from this study of *Neotrigonia*, therefore, is of a group of bivalves with similarities to representatives of almost every major bivalve subclass. They indeed appear to be living remnants of a myophorid stock from which probably all modern bivalve lineages arose (Newell, 1969). Just as important, however, they seem to be a group from which no other 'higher' forms have arisen (Douville, 1912). There is perhaps, in terms of shell structure, the lack of mantle fusions and gill structure, a closer relationship with the Palaeotaxodonta and Pteriomorphia. Certainly such a conclusion could not be countered by a lack of similarity in terms of shell structure or stomach structure. Almost just as certainly, a close affinity with the Unionacea becomes less convincing. This is especially significant if one accepts that the term 'schizodont' has "little value" (Cox, 1969). It is perhaps more significant than is currently realised that the secondary dentition on the hinge teeth of *Neotrigonia* were regarded by Stanley (1977; 1978) to be structures aiding valve alignment, in the absence of an extensive ligament, during wide valve gaping, perhaps during leaping. Perhaps if the term 'secondary' is applied more rigorously, i.e. that such serrations are truly secondary, adaptive features, then the already questionable argument of the significance of comparable striations on the schizodont dentition of the Unionacea becomes even less forceful. That is, this character in the Unionacea may also be adaptive, because of wide valve gaping.

Early students of the Trigoniacea, e.g. McMichael (1956), considered them to be "living fossils" as does Tevesz (1975). Stanley (1977; 1978) questioned the

Table 1. Comparison of eight *Neotrigonia* characters with those of other superfamilies of bivalves, representatives of which possess similar characters.

	Character	Reference	Superfamily	Sub-class	
1)	Shell structure				
	Aragonitic, three layers	Taylor *et al.*, 1969; 1973.	Nuculacea	(outer layer = complex prisms)	Palaeotaxodonta
	Outer: Prismatic (Aragonitic simple prisms*)		Pandoracea Poromyacea Pholadomyacea		Anomalodesmata
	Middle: lenticular nacre				
	Inner: sheet nacre	Ben Mlih, 1983	Mytilacea Pinnacea Pteriacea	(outer layer = Calcite simple prisms)	Pteriomorphia
	*complex prisms		Unionacea	(outer layer = Aragonitic simple prisms)	Palaeoheterodonta
2)	Hinge teeth				
	Schizodont	Cox, 1952; 1969; Newell, 1969; Newell & Boyd, 1975	Unionacea	Palaeoheterodonta	
3)	Ligament				
	parivincular, opisthodetic	Trueman, 1969	Solemyacea	Cryptodonta	
			Mytilacea Pinnacea Pteriacea	Pteriomorphia	
			Unionacea	Palaeheteodonta	
			Lucinacea Crassatellacea Cardiacea Mactracea Solenacea Tellinacea Dreissenacea Glossacea Veneracea Myacea Pholadacea	Heterodonta	
			Poromyacea Verticordiacea Pholadomyacea Pandoracea Clavagellacea	Anomalodesmata	
4)	Musculature				
	a) Equal adductors, pedal retractors + anterior pedal protractors	Various authors	Unionacea	Palaeoheterodonta	
			Arcacea	Pteriomorphia	
			Lucinacea Leptonacea Gastrochaenacea	Heterodonta	
	b) pedal elevator muscles	Pelseneer, 1911	Tellinacea Cardiacea Mactracea Solenacea Gastrochaenacea	Heterodonta	
5)	Mantle fusions				
	None	Yonge, 1957; 1982	Nuculacea	Palaeotaxodonta	
			Arcacea Limopsacea Pinnacea Pteriacea Pectinacea Anomiacea Limacea Ostreacea	Pteriomorphia	

6) Ctenidia			
a) filibranch	Ridewood, 1903; Atkins, 1938	Arcacea	Pteriomorphia
		Limopsacea	
		Mytilacea	
		Pteriacea	
		Pectinacea	
		Anomiacea	
b) homorhabdic/non plicate	Atkins, 1938	Arcacea	Pteriomorphia
c) Posterior ends of ctenidia unattached	Various authors	Arcacea	Pteriomorphia
		Limopsacea	
		Pteriacea	
		Pectinacea	
		Anomiacea	
		Limacea	
		Ostreacea	
d) Ciliary fusion of dorsal edge of ascending lamellae to visceral mass or mantle	Atkins, 1937a,c; 1938	Nuculacea	Palaeotaxodonta
		Anomiacea	Pteriomorphia
		Pteriacea	
		Pinnacea	
		Arcacea	
	Morton, 1985	Pholadomyacea	Anomalodesmata
		Pandoracea	
		Thraciacea	
		Clavagellacea	
e) Gill ciliation, type B(1b)	Atkins, 1937b	Pteriacea	Pteriomorphia
		Pectinacea	
		Limacea	
		Ostreacea	
f) Macrociliobranchia	Atkins, 1938	Nuculacea	Palaeotaxodonta
		Nuculanacea	
		Solemyacea	Cryptodonta
		Mytilacea	Pteriomorphia
		Ostreacea	
		Unionacea	Palaeoheterodonta
		Lucinacea	Heterodonta
		Leptonacea	
		Crassatellacea	
		Cardiacea	
		Mactracea	
		Solenacea	
		Tellinacea	
		Dreissenacea	
		Arcticacea	
		Corbiculacea	
		Veneracea	
		Myacea	
		Gastrochaenacea	
		Hiatellacea	
		Pholadacea	Anomalodesmata
		Pandoracea	
		Thraciacea	
		Pholadomyacea	
		Clavagellacea	
7) Ctenidial/labial palp junction Category I	Stasek, 1983	Nuculacea	Palaeotaxodonta
		Mytilacea	Pteriomorphia
		Unionacea	Palaeoheterodonta
		Crassatellacea	Heterodonta
8) Stomach structure Type IV	Purchon, 1957; 1958; 1960a	Pectinacea	Pteriomorphia
		Anomiacea	
		Limacea	
		Unionacea	Palaeoheterodonta
		Carditacea	Heterodonta
		Crassatellacea	
		Gastrochaenacea	
		Hiatellacea	
		Pandoracea	Anomalodesmata
		Clavagellacea	
		Thraciacea	

validity of this term in defining a group of Mesozoic bivalves with living representatives, that would, but for unknown extinction forces, constitute an important ecological group in near shore habitats world wide. Semantics aside, however, it would seem to this author that the term 'living fossil' might be appropriately applied to the Trigoniacea, because as this study suggests they possess many remarkable characters which in combination must reflect very early bivalve features. Notable among these are the ctenidial ciliation and the lack of pallial fusions. So early, in fact, that their ancestors, the Myophoridae, have been viewed as the stem group for perhaps most of today's living members of the Bivalvia. If this is so, then the Trigoniacea are 'living fossils', closely allied with the extinct Myophoridae and Modiomorphida, sharing shell and ctenidial features with the Palaeotaxodonta, but just as importantly having a clear affiliation with the Pteriomorphia. The Unionacea, as Purchon (1978) points out, might be linked to the Heterodonta. This suggestion needs further investigation, but the essential conclusion this study reaches is that the Trigoniacea seem to represent another line of pteriomorph evolution, perhaps sharing some remote palaeotaxodont ancestor with the Unionacea, but in no greater sense than that the common ancestors of the two were probably also the ancestors of most other living bivalves.

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References

Atkins, D., 1937a. On the ciliary mechanisms and interrelationships of Lamellibranchs. Part I: New observations on sorting mechanisms. Quarterly Journal of Microscopical Science 79: 181—308.

_____ 1937b. On the ciliary mechanisms and interrelationships of Lamellibranchs. Part III: Types of lamellibranch gills and their food currents. Quarterly Journal of Microscopical Science 79: 375—421.

_____ 1937c. On the ciliary mechanisms and interrelationships of Lamellibranchs. Part IV: Cuticular fusion, with special reference to the fourth aperture in certain lamellibranchs. Quarterly Journal of Microscopical Science 79: 423—445.

_____ 1938. On the ciliary mechanisms and interrelationships of Lamellibranchs. Part VII: Latero-frontal cilia of the gill filaments and their phylogenetic value. Quarterly Journal of Microscopical Science 80: 345—436.

Ben Mlih, A., 1938. Organization de la phase carbonatée dans les prismes de *Neotrigonia margaritacea* Lmk. Comptes Rendus. 296 Series III: 313—318.

Boss, K.J., 1982. Mollusca. **In** 'Synopsis and Classification of Living Organism' (ed. S.P. Parker): 945—1166. McGraw Hill Book Company, New York.

Cox, L.R., 1952. Notes on the Trigoniidae, with outlines of a classification of the family. Proceedings of the Malacological Society of London 29: 45—69.

_____ 1960. Thoughts on the classification of the Bivalvia. Proceedings of the Malacological Society of London 34: 60—88.

_____ 1969. General features of the Bivalvia. **In** 'Treatise on Invertebrate Paleontology'. Part N, Mollusca 6 (Bivalvia) (ed. R.C. Moore): N2—129. Geological Society of America and University of Kansas Press, Lawrence, Kansas.

Darragh, T.A., 1986. The Cainozoic Trigoniidae of Australia. Alcheringa 10: 1—34.

Douville, H., 1912. Classification des Lamellibranches. Bulletin de la Société Géologique de France, iv. 12: 419—467.

Fleming, C.A., 1964. History of the bivalve family Trigoniidae in the south-west Pacific. Australian Journal of Science 26: 196—203.

Gould, S.J., 1969. The byssus of trigonian clams: phylogenetic vestige or functional organ. Journal of Paleontology 43: 1125—1129.

Gould, S.J. & C.C. Jones, 1974. The pallial ridge of *Neotrigonia:* functional siphons without mantle fusion. The Veliger 17: 1—7.

Grobben, C., 1900. Expedition S.M. Schiff 'Pola' in das Rothe Meer, XX, Morphologie und Anatomie von Meleagrina source der Aviculiden im allgemeinen. Wien.

Habe, T., 1985. On the species of the genus *Neotrigonia*. Venus 15: 98—100. (In Japanese).

Lycett, J., 1879. A monograph of the British fossil Trigoniae Palaeontographical Society. Adlard, London.

McMichael, D.F., 1956. *Neotrigoniax* — a living fossil. The Australian Museum Magazine 1956: 82—84.

Morris, N.J., 1978. The infaunal descendants of the Cycloconchidae: an outline of the evolutionary history and taxonomy of the Heteroconchia, superfamilies Cycloconchacea to Chamacea. Philosophical Transactions of the Royal Society Series B. 284: 259—275.

Morton, B., 1985. Adaptive radiation in the Anomalodesmata. **In** 'The Mollusca'. Vol. 10, Evolution (eds. K.M. Wilbur, M. Clarke & E.R. Trueman): 405—459. Academic Press, New York.

_____ 1987. The functional morphology of the organs of the mantle cavity of *Perna viridis* (Linnaeus, 1758) (Bivalvia: Mytilacea). American Malacological Bulletin 5: 161—166.

Neumayr, M., 1884. Zur Morphologie des Bivalvenschlosses. Sitzungsberichte der Akademie der Wissenschaften in Wien 88: 385—418.

———— 1889. Uber die Herkunft der Unioniden. Sitzungsberichte der Akademie der Wissenschaften in Wien 98: 5—27, pls 1—3.

Newell, N.D., 1969. Classification of Bivalvia. **In** 'Treatise on Invertebrate Paleontology'. Part N, Mollusca 6 (Bivalvia) (ed. R.C. Moore): 205—218. Geological Society of America and University of Kansas Press, Lawrence, Kansas.

Newell, N.D. & D.W. Boyd, 1975. Parallel evolution in early trigonacean bivalves. Bulletin of the American Museum of Natural History 154: 53—162.

Pelseneer, P., 1891. Contribution a l'etude les Lamellibranches. Archives de Biologie 11: 147—312.

———— 1911. Les Lamellibranches de l'expedition du Siboga, Partie Anatomique. Siboga Expeditie Monograph 53a.

Purchon, R.D., 1957. The stomach in the Filibranchia and Pseudolamellibranchia. Proceedings of the Malacological Society of London 129: 27—60.

———— 1958. The stomach in the Eulamellibranchia; stomach type IV. Proceedings of the Malacological Society of London 131: 487—525.

———— 1960a. The stomach in the Eulamellibranchia; stomach types IV and V. Proceedings of the Malacological Society of London 135: 431—489.

———— 1960b. Phylogeny in the Lamellibranchia. Proceedings of Centenary and Bicentenary Congress of Biology, Singapore, 1958: 69—82.

———— 1978. An analytical approach to a classification of the Bivalvia. Philosophical Transactions of the Royal Society Series B, 284: 425—436.

Ridewood, W.G., 1903. On the structure of the gills of lamellibranchs. Philosophical Transactions of the Royal Society Series B, 194: 147—284.

Smith, D.C., 1983. On the so-called mantle muscle scars on shells of the Margaritiferidae (Mollusca, Pelecypoda), with observations on mantle-shell attachment in the Unionoida and Trigonioida. Zoologica Scripta 12: 67—71.

Stanley, S.M., 1968. Post-Paleozoic adaptive radiation of infaunal bivalve molluscs — a consequence of mantle fusion and siphon formation. Journal of Paleontology 42: 214—229.

———— 1977. Coadaptation in the Trigoniidae, a remarkable family of burrowing bivalves. Paleontology 20: 869—899.

———— 1978. Aspects of the adaptive morphology and evolution of the Trigoniidae. Philosophical Transactions of the Royal Society Series B, 284: 247—258.

Stasek, C.R., 1963. Synopsis and discussion of the association of ctenidia and labial palps in the bivalved Mollusca. The Veliger 6: 91—97.

Steinmann, J.H.C.G.G., 1903. Einfuhrung in die Palaontologie Leipzig, 466 pp.

Taylor, J.D., W.J. Kennedy & A. Hall, 1969. The shell structure and mineralogy of the Bivalvia. Introduction. Nuculacea — Trigonacea. Bulletin of the British Museum of Natural History (Zoology), Supplement 3: 1—125, pls 29.

———— 1973. The shell structure and mineralogy of the Bivalvia. II Lucinacea — Clavagellacea. Conclusions. Bulletin of the British Museum Natural History (Zoology) 22(9): 255—294, pls 15.

Tevesz, M.J.S., 1975. Structure and habits of the "living fossil" pelecypod *Neotrigonia*. Lethaia 8: 321—327.

Trueman, E.R., 1969. Ligament. **In** 'Treatise on Invertebrate Paleontology'. Part N, Mollusca 6 (Bivalvia) (ed. R.C. Moore): 58—64. Geological Society of America and University of Kansas Press, Lawrence, Kansas.

White, K.M., 1942. Pericardial cavity and the pericardial gland of the Lamellibranchia. Proceedings of the Malacological Society of London 25: 37—88.

Yonge, C.M., 1957. Mantle fusion in the Lamellibranchia. Pubbicazioni della Stazione zoologica di Napoli 29: 25—31.

———— 1982. Mantle margins with a revision of siphonal types in the Bivalvia. Journal of Molluscan Studies 48: 102—103.

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Australian Species of *Nerocila* Leach, 1818, and *Creniola* n. gen. (Isopoda: Cymothoidae), Crustacean Parasites of Marine Fishes

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ABSTRACT. The genus *Nerocila* is rediagnosed, and the Australian species revised and redescribed in full. Species represented are *Nerocila orbignyi* (Guérin-Méneville), *N. congener* Miers, *N. phaiopleura* Bleeker, *N. barramundae* n. sp., *N. lomatia* n. sp., *N. monodi* Hale, *N. serra* and *Nerocila* sp. The genus *Emphylia* Koelbel is synonymised with *Nerocila.* The new genus *Creniola* is created for the species *C. laticauda* (Schiödte & Meinert), *C.saurida* (Avdeev), and *C. breviceps* (Schiödte & Meinert) from Hawaii.

Several new synonymies are reported: *Nerocila cebuana* Schiödte & Meinert and *Nerocila philippinensis* Bovallius are synonymised with *N. congener; Nerocila laevinota* Miers is synonymised with *N. sundaica* Bleeker; *Nerocila maculata, N. affinis, N. adriatica, N. australasiae, N. cephalotes, N. macleayii, N. neapolitana, N. novaezelandiae, N. tartowskii, N. trailli, N. laticeps, N. vittata* and *Rosca rogans* are placed in synonymy with *Nerocila orbignyi.* The history of *Nerocila orbignyi* is fully discussed, and the species is distinguished from related species. The following species are regarded as *nomina dubia: N. aculeata* Dana, *N. aculeata* Edwards, *N. falklandica* Cunningham, *N. brasiliensis* Dana, *N. latiuscula* Dana, *N. tenuipes* Dana, *N. brongnartii* (Risso) and *N. cuspidata* Costa. The subfamily Anilocrinae Schiödte & Meinert is rediagnosed. Host preferences, morphological variability and distribution are discussed.

Notes and some figures are given on other poorly known Indo-Pacific genera, and a list of all species of *Nerocila* is provided. A key to the Indo-Pacific genera of Anilocrinae, and keys to the Australian species of *Nerocila* and *Creniola* are provided.

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This is the third study of a series dealing with Australian genera and species of the externally attaching lineage of the Cymothoidae. The two previous works (Bruce, 1987a, 1987b) dealt with the genera *Anilocra* Leach, *Pleopodias* Richardson and *Renocila* Miers.

Nerocila poses some special problems compared with related genera. While most cymothoids are considered to be morphologically more variable than other flabelliferan families, recent work (Bruce, 1986, 1987a, b; Williams & Williams, 1980, 1981) has shown that once taxonomically useful species characters have been discerned the variation is far less than previously supposed. This is not the case for *Nerocila.* Variation within *Nerocila* is not yet fully documented, but certain species are very variable. The species for which variability has been documented, at least in part, are: *Nerocila acuminata* (see Brusca, 1981); *Nerocila sundaica* (in excellent detail by Bowman, 1978); *Nerocila armata* and *Nerocila orbignyi* (Monod, 1931); *Nerocila orbignyi, Nerocila monodi, Nerocila phaiopleura* (present study). As is demonstrated here by *Nerocila orbignyi* from Walpole, WA, this variation occurs within a single isopod population, that is from one host species in one locality. Variation can rarely be correlated to geographic, host or habitat differences.

The problems caused by such variability are exemplified by the complex and lengthy synonymy for *Nerocila orbignyi,* where 16 species names are placed in synonymy, including two *nomina nuda,* three *nomina dubia,* and a further two probable synonyms. Because of this variability and the inadequacy of the many earlier descriptions, there are several species in the literature that cannot reliably be recognised. To try to bring some order into this genus I have provided an annotated list of all current species names for *Nerocila,* with notes on their current status, need of revision, and most useful recent literature. In some cases supplementary figures have been given to assist in species recognition.

Use of subfamily names within the Cymothoidae has been erratic. In their monograph Schiödte & Meinert (1879—1884) proposed the following classification.

Cymothoarum (= superfamily Cymothoidea)
Aegidae Dana
Anilocridae Schiödte & Meinert
Saophridae Schiödte & Meinert
Cymothoidae Leach
Tribe Ceratothoinae (= subfamily)
Tribe Cymothoinae
Tribe Lironecinae

This classification was little used by later workers, all of whom recognised the Aegidae and Cymothoidae as two readily distinguished families within the Flabellifera, and the Anilocridae and Saophridae as part of the Cymothoidae. Of recent workers only Trilles (e.g. 1979) has consistently followed Schiödte & Meinert's (1881—1884) system, using the family names Anilocridae and Cymothoidae but placing them within Cymothoidae. Schiödte & Meinert's classification was highly perceptive, recognising the major difference between genera attaching externally (*Anilocra* and related genera) and those attaching to the gills or in the mouth ('Cymothoidae'). Within the latter they recognised three clear generic groups (Schiödte & Meinert's (1883) family Saophridae clearly belongs within their

Ceratothoinae). Their classification is supported in part by Brusca's (1981) analysis which recognises a major division between the gill/buccal lineage (= Cymothoidae and Saophridae) and the externally attaching lineage (= Anilocridae).

I propose to recognise the subfamily Anilocrinae and offer a diagnosis that separates it from other genera. At present I do not intend to attempt to define another subfamily (other than by 'not Anilocrinae'). There is at present a lack of understanding of cymothoid characters, and the larger genera *Lironeca, Ceratothoa, Cymothoa* and most of their species, are urgently in need of revision. Until detailed description of the greater proportion of species has been undertaken, generic characters cannot be assessed, and similarly for genera on an analysis of subfamily characters. Notwithstanding, it is evident to most who study the Cymothoidae that the gill attaching and buccal attaching genera form two distinct groups. Convergence can be argued, but when a species of a gill attaching genus (e.g. *Mothocya ihi* Bruce, 1986) secondarily becomes buccal attaching, it still retains the essential characters of the gill attaching genera. Similarly, *Nerocila lomatia* which attaches in the gill cavity cannot be confused with genera such as *Lironeca* or *Mothocya.*

Methods

Methods used follows Bruce (1987a), with the notable exceptions that no new material was obtained by personal collecting and that no specimen (other than *N. lomatia)* was examined in association with its host. Many of the isopods examined here are from trawled or netted fish. *Nerocila* species (and many other cymothoids) detach readily when the host is removed from water, and the possibility exists that some host records may be erroneous. Repeated records from the same host are regarded as good evidence of actual host use. No host identifications were made by the Australian Museum fish section, and are presumed to have been made by the collectors. All host names have been confirmed by the Australian Museum fish section.

All isopod length measurements are in millimetres.

Abbreviations

AM	Australian Museum, Sydney, NSW, Australia
BMNH	British Museum (Natural History), London
MCZ	Museum of Comparative Zoology, Harvard University, Massachussetts, USA
MNHN	Muséum National d'Histoire Naturelle, Paris, France
NMV	Museum of Victoria, Melbourne, Australia
NRS	Naturhistoriska Riskmuseet, Stockholm, Sweden
NMW	Naturhistorisches Museum, Vienna
NSW	New South Wales, Australia
NSW SF	New South Wales State Fisheries
NT	Northern Territory, Australia
NTM	Northern Territory Museum, Darwin, Australia
Qld	Queensland, Australia
QM	Queensland Museum, Brisbane, Australia
SA	South Australia
SAM	South Australian Museum, Adelaide, Australia
Tas	Tasmania, Australia
USNM	Smithsonian Institution (Natural History), Washington, D.C., USA
Vic	Victoria, Australia
WA	Western Australia
WAFRI	West African Fisheries Research Institute
WAM	Western Australian Museum, Perth, Australia
ZMA	Zoologisch Museum, University of Amsterdam, Nederlands
ZMB	Zoologisches Museum der Humboldt-Universitat zu Berlin, Deutsch Demokratische Republic
ZMC	Zoologisk Museum, Copenhagen, Denmark.

Host Preferences of *Nerocila* and *Creniola*

The host records for Australian *Nerocila* are summarised in Table 1. From this and the accounts of Brusca (1981) and Trilles (1975b) it can be seen that *Nerocila* species show little preference to a particular host family or genus. This contrasts strongly with the available data for *Anilocra* (Bruce, 1987a; Williams & Williams, 1981) and *Renocila* (Bruce, 1987b; Williams & Williams, 1980). *Nerocila monodi* is here recorded from five host families (seven species in seven genera), and *Nerocila orbignyi* from 11 host families (ten species in ten genera). In contrast only three species of *Anilocra* were found on two host families, the other three occurring only on one family (Bruce, 1987a).

The closest approximation to specificity is that in certain areas a particular host may be more commonly used. In southern Western Australia *Nerocila orbignyi* is most frequently recorded from *Pseudocaranx dentex.* In Queensland *Nerocila monodi* is most often recorded from species of Sparidae. Similarly Bowman and Tareen (1983) found that *Nerocila phaiopleura* occurs most often on species of Clupeoidea. The two Australian species of *Creniola* both utilise benthic hosts associated with soft bottom habitats.

Position on the host has not been widely recorded, but is most commonly the caudal peduncle (a position

occasionally used by some *Anilocra* species) or attached to the base of pectoral or dorsal fin. Table 1 presents a list of known hosts of Australian species of *Creniola* and *Nerocila.*

Distribution

The distribution of Australian *Nerocila* species is shown in Figs 29 and 30, and that of *Creniola* in Fig. 31. Two species have an extensive southern distribution: *Nerocila orbignyi* and *Creniola laticauda,* both extending from southern Western Australia to central New South Wales. *Creniola laticauda* is endemic to southern Australia. *Nerocila orbignyi* occurs from New Zealand and southern Australia to South Africa, and along the eastern Atlantic north to Holland and east into the Mediterranean.

All of the remaining species occur north of about 30°S. Of these, three are known only from Australia: *N. barramundae, N. lomatia* and *N. monodi.* All three have wide distribution within Australia. *Creniola saurida, Nerocila congener* and *N. phaiopleura* are widely distributed Indo-West Pacific species.

Latitudinally the greatest diversity is found within the tropics, as is also shown by the genera *Anilocra* and *Renocila.* The genus *Nerocila* is more successful in colonising temperate waters than other anilocrine genera, and in Australia is the only genus with representatives occurring south of about 27°S.

Taxonomy

Anilocrinae Schiödte & Meinert, 1881

Diagnosis. Cephalon not deeply immersed in pereonite 1. Pleonite 1 always as wide as pleonite 2. Pleonites ventrally extended. Antennule basal articles (1—3) distinctly wider than remaining articles. Maxilla medial lobe partly fused to lateral lobe. Pereopods with basis never expanded, articles never dilated. Brood pouch formed of two major oostegites arising from coxae 6 (other oostegites small) and posterior pocket. Pleopod 5 endopod with 2 or 3 complexly folded lobes, distal margin indented.

Type genus. The genus *Anilocra* Leach, 1818, is the type genus for the subfamily.

Table 1. Australian species of *Nerocila* and *Creniola* and their associated hosts. (* = isopod specimens not seen; + name not confirmed).

ISOPOD		HOSTS	LOCALITIES
Creniola laticauda	Platycephalidae	*Platycephalus richardsoni* *	Off Coffs Harbour, NSW (Hooper, 1983)
		Platycephalus sp.	Off Montague Island, NSW
	Zeidae	*Zeus* sp.	Off Kiama, NSW
	Rajidae	*Raja australis* *+	Port Willunga, S.A. (Hale, 1926)
Creniola saurida	Synodidae	*Saurida tumbil*	Moreton Bay, Qld.
	Scorpaenidae	*Hypodytes carinatus*	Arafura Sea, NT
	Tetraodontidae	*Spheroides multistriatus*	North Qld.
	Triglidae	*Satyrichthyes welchi*	Qld Coral Sea
Nerocila barramundae	Latidae	*Lates calcarifer*	Gulf of Carpentaria
	Lobotidae	*Lobotes surinamensis*	Rockhampton, Qld.
Nerocila lomatia	Clupeidae	*Pellona ditchella*	Townsville, Qld.
	Mugilidae	*Mugil georgii*	Moreton Bay, Qld.
Nerocila monodi	Carangidae	*Carangoides humerosus*	Arafura Sea, NT
	Lutjanidae	*Lutjanus sp.*	Palm Group, Qld.
	Nemipteridae	*Nemipterus hexodon*	Arafura Sea
	Pomadasidae	*Pomadasys hasta*	Townsville, Qld.
	Priacanthidae	*Priacanthus macracanthus*	Moreton Bay, Qld.
	Sparidae	*Acanthopagrus australis*	Southeast Qld.
		Chrysophrys auratus	Southeast Qld.
		Rhabdosargus sarba	Tin Can Bay, Qld.
Nerocila orbignyi	Callorhynchidae	*Callorhynchus milii*	Bass Strait
	Carangidae	*Pseudocaranx dentex*	Southern WA
	Dactylopenidae	*Dactylopena orientalis*	South Coast, Tas.
	Kyphosidae	*Girella tricuspidata* *	Lake Illawarra, NSW (O'Connor, 1978)
	Molidae	*Mola mola*	Off NSW
	Mugillidae sp.		Port Hacking, NSW
	Platycephalidae sp.		Victoria
	Pomatomidae	*Pomatomus saltatrix*	Nornalup, WA
	Silliganidae	*Sillago bassensis*	Tasmania
	Sparidae	*Acanthopagrus butcheri*	The Coorong, SA
		Chrysophrys auratus	Sydney area, NSW
	Triglidae	*Chelidonichthye kumu*	Off Eden, NSW
Nerocila phaiopleura	Mugilidae	*Liza argentea*	Proserpine, Qld.
	Engraulidae	*Engraulis australis*	Swan River, WA
	Plotosidae	*Cnidoglanus macrocephalus*	Swan River, WA

Remarks. Brood pouch morphology has been ignored by taxonomic workers. Only one report (Trilles, 1973b) compares the brood pouch of different genera, and other than in Bruce (1986) it remains undescribed and unfigured for all species. This is in contrast to the Sphaeromatidae where brood pouch morphology is a major generic character (Harrison, 1984).

Within the Cymothoidae there are two types of brood pouch. The Anilocrinae have a brood pouch formed from overlapping pairs of oostegites arising from coxae 1—4 and 6, those of coxae 6 being very large, and forming the part of the marsupium which contains the developing embryos. The remaining oostegites are very much smaller, and those of coxae 1—3 do not enclose embryos in *Anilocra* and *Nerocila*. The posterior of the brood pouch is enclosed by a laminar posterior pocket formed from the posterior of sternite 7. This flap occupies the full width at the posterior and extends anteriorly beneath the oostegites. The flap is considerably thicker than the oostegites. Figures 1A—C illustrates its shape in three anilocrine genera.

In the other marine genera the brood pouch is formed by paired oostegites arising from coxae 1—4 and 6, 1—5 or 2—5, but all oostegites form part of the marsupium. There is no posterior pocket, and the oostegites of coxae 6 curve under to enclose the marsupium. Such a brood pouch occurs in *Mothocya* (figured by Bruce, 1986), *Cterissa* (Trilles & Paperna, 1980), *Lironeca* (Fig. 1E) and *Ceratothoa* (Fig. 1D, and photographs of Trilles, 1973a), *Cymothoa*

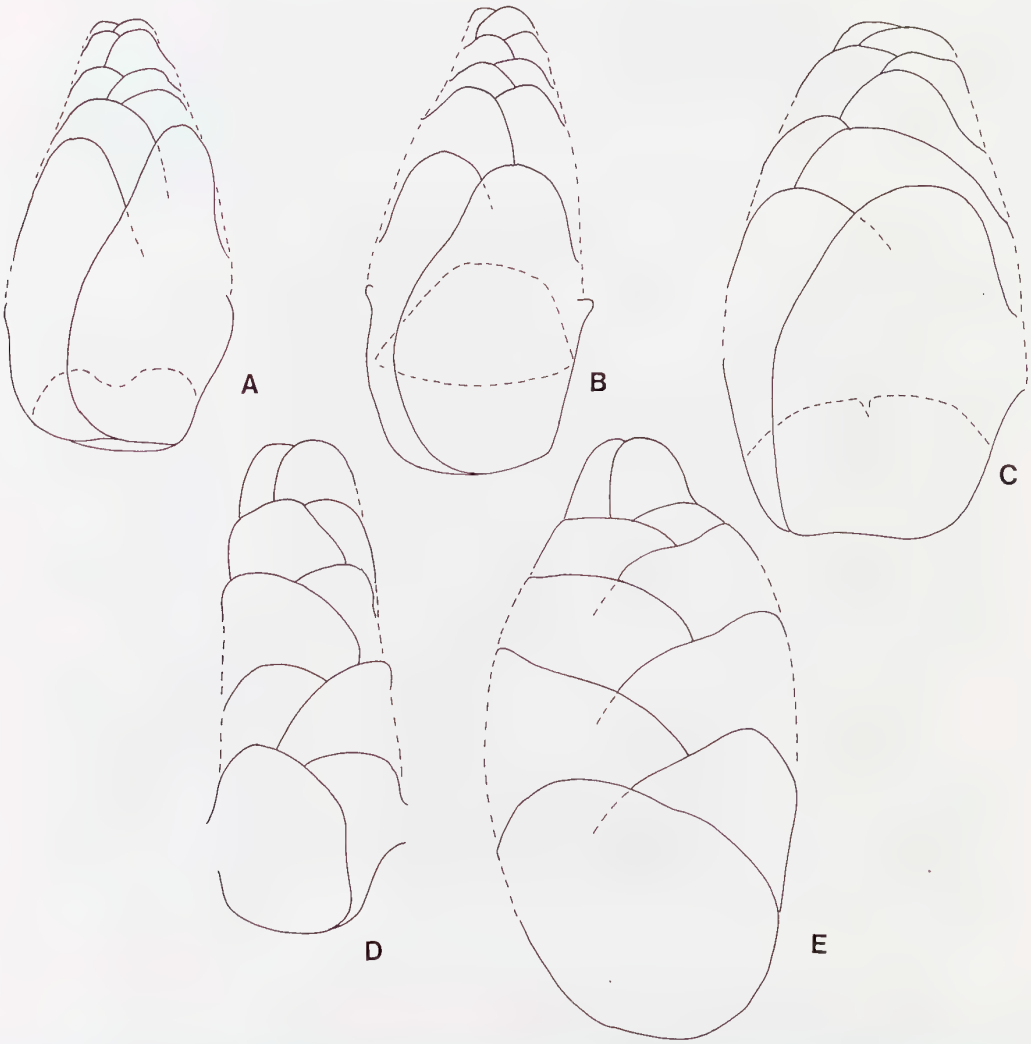

Fig. 1. Brood pouches: **A,** *Anilocra nemipteri* Bruce (AM P37824); **B,** *Nerocila orbignyi* (AM P37149, female #2); **C,** *Renocila ovata* Miers (WAM 611-85); **D,** *Ceratothoa trigonocephalon* (Leach, 1818) (AM P37262); **E,** *Lironeca raynaudii* Edwards (AM P37780).

(photographs of Trilles, 1975c).

Coupled with the differences in brood pouch morphology are the differences in pleon and pleopod morphology (Fig. 2). Anilocrinae have pleon lateral margins extending, partly concealing the pleopod peduncles in lateral view. No Anilocrinae has narrow pleonites 1 or 2, a common condition in other genera. The genera *Anilocra, Nerocila* and *Creniola* have lobes on the posterior surface of the endopods of pleopods 3 and 4, and the endopod of pleopod 5 complexly folded; pleopods 3—5 have the endopod proximomedial lobe folded (these pleopod characters are less developed in *Pleopodias* and *Renocila).* In contrast the pleopods of *Mothocya* (see Bruce, 1986), *Lironeca* (most species), *Ceratothoa,* and *Cymothoa* (there are virtually no figures available for *Cymothoa* pleopods except those of Brusca, 1981) are all essentially laminar.

At present there is insufficient descriptive data on many cymothoid genera, and it is probable that as other genera are revised, some will be found to belong to the Anilocrinae. *Lironeca convexa* (see Brusca,

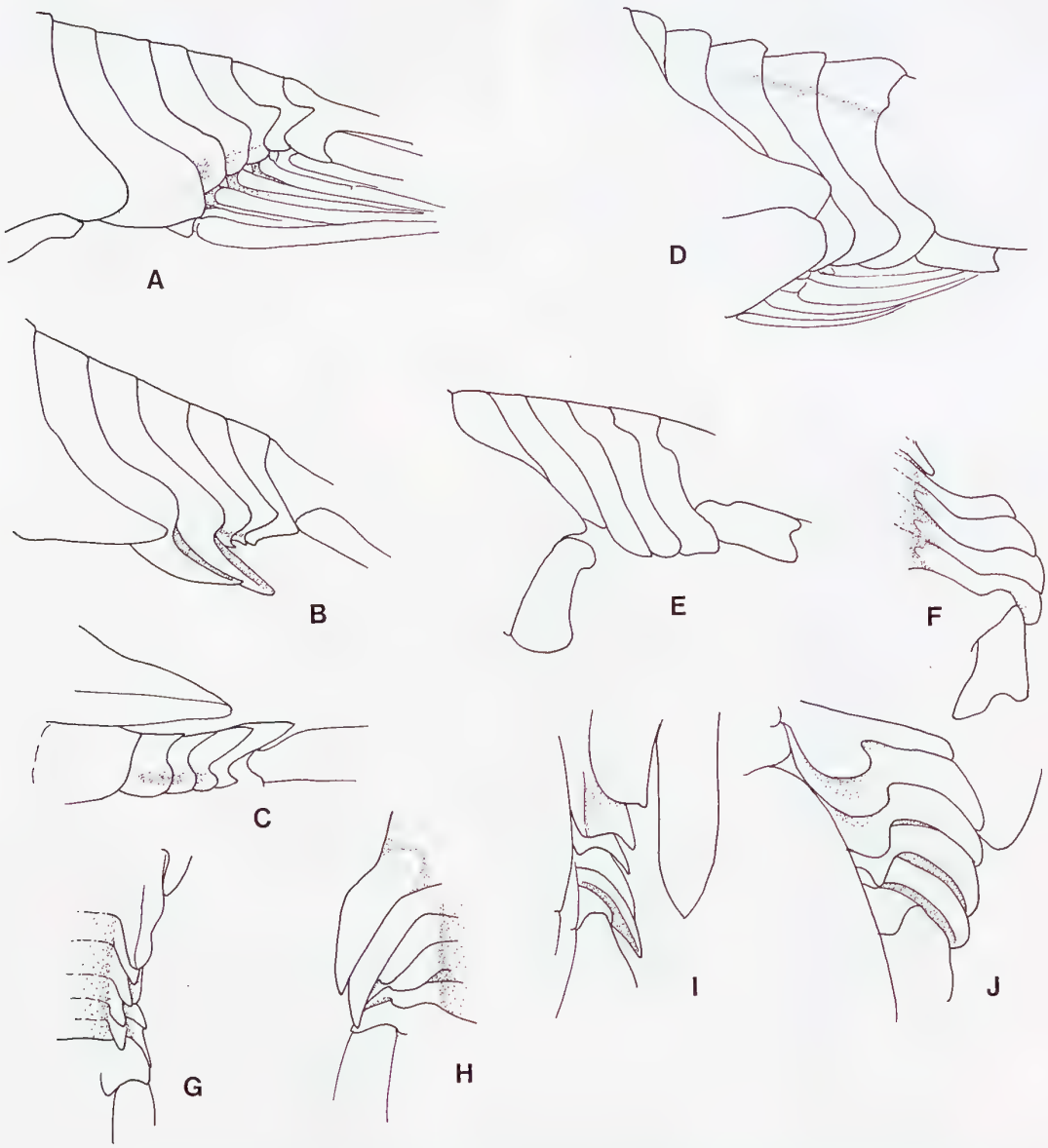

Fig. 2. Pleon morphology: A—E, lateral view; F—J, ventral view. **A,** *Anilocra nemipteri* (AM P37824); **B,** *Nerocila orbignyi* (AM P37149, female #2); **C,** *Renocila ovata,* ventrolateral view (WAM 611-85); **D,** *Lironeca raynaudii* (AM P37780); **E,** *Ceratothoa trigonocephalon* (AM P37262); **F,** *Ceratothoa trigonocephalon;* **G,** *Anilocra nemipteri;* **H,** *Nerocila orbignyi;* **I,** *Renocila ovata;* **J,** *Lironeca raynaudii.*

1981) has a pleopod and pleon morphology that suggests it would be better placed in the Anilocrinae. I examined the type material of *Enispa irregularis* (Bleeker) which similarly has a brood pouch, pleonal, pereopodal and pleopod morphology that conforms to the Anilocrinae. *Enispa* needs to be fully rediagnosed before it can formally be transferred to the Anilocrinae.

The division of the Cymothoidae into three "lineages" has been suggested by Brusca (1981). The lineages are essentially externally attaching genera, the gill-buccal genera and the paraphyletic (Brusca 1981) flesh burrowing genera. Although it is possible to unambiguously define the Anilocrinae, substantial revisionary work is required before the gill-buccal and flesh burrowing lineages can be diagnosed and their status assessed.

Although few data are available on character state polarity within the Cymothoidae, certain characters given in the diagnosis above can be recognised as apomorphic and unique to the Anilocrinae: brood pouch with the anterior oosategites reduced and with a posterior pocket; maxilla medial lobe fused to lateral; pleopod 5 with massively folded endopod.

Figures of the brood pouch are given for *Nerocila* and *Renocila,* and for the genera *Lironeca* and *Ceratothoa* (Fig. 1). Pleon morphologies for the anilocrine genera, and the genera *Lironeca, Ceratothoa* are given in (Fig. 2).

Key to the Indo-Pacific Genera of Anilocrinae

1. Cephalon posterior margin trisinuate; coxae 5—7 as long as, or longer than respective pereonite (except *N. lomatia).* 2

——Cephalon posterior margin not trisinuate; coxae 5—7 manifestly shorter than respective pereonite. 5

2. Pleonites 1 and 2 ventrolateral margins produced. ..... *Nerocila*

——Pleonites 1 and 2 ventrolateral margins not produced. 3

3. Body dorsal surface strongly vaulted; coxae 5—7 ventrally directed; pleonites strongly produced ventrally. ..... *Plotor*

——Body dorsal surface weakly vaulted; coxae 5—7 posteriorly directed; pleonites not strongly produce ventrally. 4

4. Uropod rami long, extending well beyond posterior of pleotelson; coxae conspicuous in dorsal view. ..... *Amblycephalon*

——Uropod rami short, not extending beyond posterior of pleotelson; coxae inconspicuous in dorsal view. ..... *Creniola*

5. Cephalon without rostrum, or rostrum not projecting between antennule bases; antennule as long as, or longer than antenna; posterolateral margins of pereonites 5—7 produced; coxae 5—7 posteriorly acute. ..... *Renocila*

——Rostrum folded under, projecting between antennule bases; antennule shorter than antenna; posterolateral margins of pereonites 5—7 not produced; coxae posteriorly rounded. 6

6. Mandible palp article 3 shorter than article 2; maxilla with 2 short spines each on medial and lateral lobe, medial lobe partly fused to lateral; antennule articles 4—8 short; pleonites 3—5 or 4—5 about 0.7 width of pereon. ..... *Anilocra*

——Mandible palp article 3 longer than article 2; maxilla with 2 large nodular spines each on medial and lateral lobe, medial lobe distinct; antennule articles 4—8 elongate; pleonites 3—5 or 4—5 about 0.45 width of pereon. ..... *Pleopodias*

Indo-Pacific Genera of Anilocrinae

Only two Indo-Pacific genera of the subfamily have not been recorded from Australian waters. *Rosca* (included in the key given by Bruce, 1987a) was synonymised with *Renocila* by Bruce (1987b).

Amblycephalon Pillai, 1954. The genus has a trilobed posterior margin to the cephalon which places it, in the key, among the genera allied to *Nerocila. Nerocila schadleri* Nierstrasz, 1915 agrees well with Pillai's (1963) diagnosis and is here transferred to *Amblycephalon.* Both *A. indicus* Pillai,

1954 and *A. schadleri* are in need of redescription before their status can be ascertained. Additional figures of the type of *Amblycephalon schadleri* n. comb. are given here (Fig. 3).

Plotor Schiödte & Meinert, 1881. Additional figures from the types are given here (Fig. 4). Known only from the type locality. The antennule of this species is longer and more robust than the antenna.

Fig. 3. *Amblycephalon schadleri* (Nierstrasz). Holotype (RMNH 8), Kisser, Irian Jaya, Indonesia, 1898, coll. H. Schadler. **A,** dorsal view; **B,** lateral view; **C,** frons; **D,** pereopod 6; **E,** pereopod 7; **F,** pereopod 3; **G,** uropod. All appendages drawn in situ. Scale line 4.0 mm.

Nerocila Leach

Nerocila Leach 1818: 351.—Desmarest, 1825: 307; Edwards, 1840: 250; Dana, 1853: 747; Schiödte & Meinert, 1881: 4; Gerstaecker, 1882: 231; Richardson, 1905: 219; Hale, 1926: 202; Monod, 1931: 5; Van Name, 1936: 431; Barnard, 1936: 163; Brian & Dartevelle, 1949: 135; Szidat, 1955: 216; Kensley, 1978: 82; Kussakin, 1979: 275; Brusca, 1981: 150; Menzies & Kruczynski, 1983: 55; Brusca & Iverson, 1985: 45.
Ichthyophilus Latreille, 1802: 133.
Emphylia Koelbel, 1879: 413
Pterisopodus Boone, 1918: 596.
Nerocila (Emphylia).—Miers, 1880: 4; Bowman, 1978: 34.

Diagnosis of female. Body 2—3 times as long as wide, dorsoventrally flattened. Cephalon anterior margin wide, not rostrate, not folded back; posterior margin distinctly trilobed. Pleon manifestly narrower than pereon (0.6—0.7); ventrolateral margins of pleonites 1 and 2 produced. Mandible palp slender, elongate, article 1 longest; article 3 as long as, or longer than 2, with setae on distolateral margin. Pleopods 1—5 peduncles with lateral lobe; endopods of pleopods 1—5 with accessory lamella on proximomedial margin, becoming large and folded on pleopods 3—5; pleopod 5 endopod with 2 or 3 large folded lobes.

Additional characters. Body widest at pereonite 6. Eyes may be obscured. Coxae well developed, usually as long as, or longer than respective pereonite, visible in dorsal view. Posterolateral margins of pereonites 5—7 usually produced. Pleotelson flat.

Antennule with 8 articles, articles 1 and 2 conspicuously larger than 3—8. Antenna slender, longer than antennule, with 9—11 articles. Maxillule with 3—5 terminal spines. Maxilla medial lobe partly fused to lateral, 2 curved spines on each lobe. Maxilliped article 3 with 3—5 spines. Pereopods 1—5 basis increasing slightly in length towards posterior. Pereopods 6 and 7 longer than 5; pereopod 7 with or without spines. Brood pouch made up of 5 pairs of oostegites arising from pereonites 1, 2, 3, 4 and 6, and posterior pocket; last pair of oostegites extend over pleopods. Endopods of pleopods 3 and 4 each with single small fold. Pleopod 2 retains appendix masculina. Uropod exopod longer than endopod; both rami extend beyond posterior margin of pleotelson.

Male. Body narrower than female, but otherwise similar except that coxae, pereonite posterolateral margins and pleonites 1 and 2 have not yet developed the full female form.

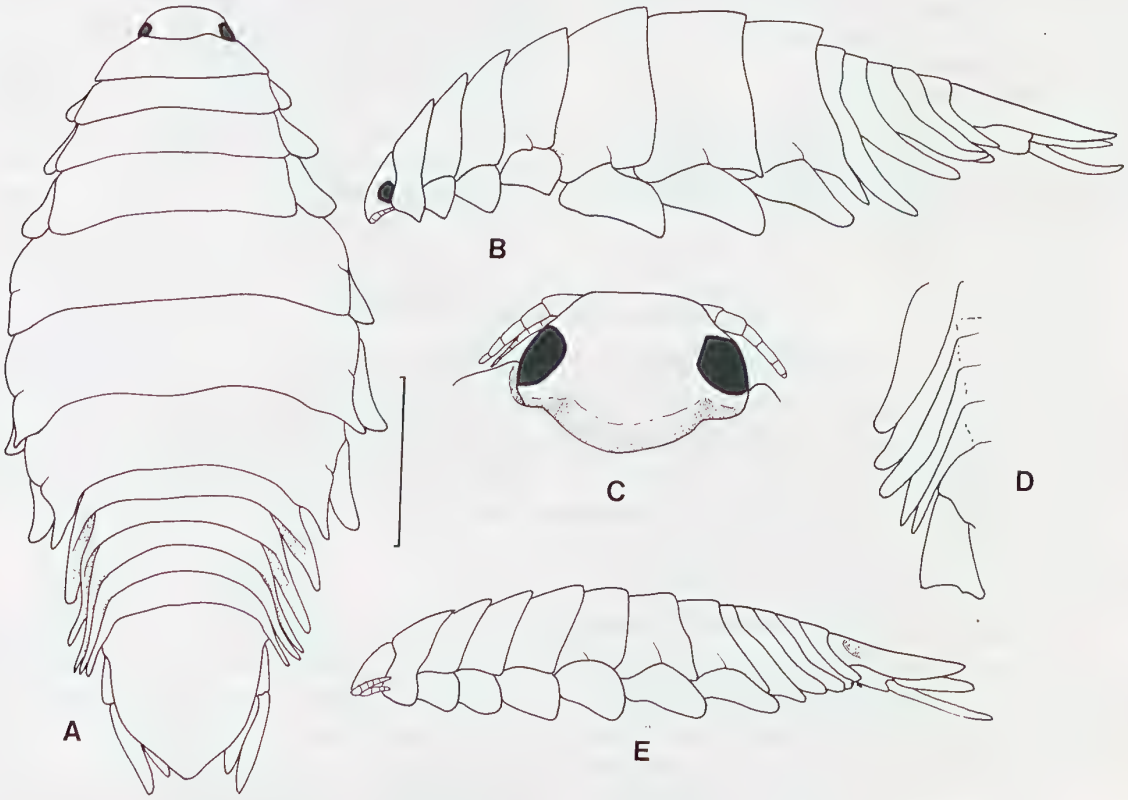

Fig. 4. *Plotor indus* Schiödte & Meinert. Female lectotype 13.5 mm, paralectotypes 11.0, 7.5 mm, 4°30′S, 37°0′E, 8 Jan 1875, Casparsen, ZMC. A—C, lectotype. **A,** dorsal view; **B,** lateral view; **C,** cephalon, dorsal view; **D,** paralectotype, 11 mm, ventral view of right pleonites; **E,** paralectotype, lateral view. Scale line 3.0 mm.

Type species. Leach (1818) clearly indicated *Nerocila blainvillii* as the single species he was placing in the genus. He also listed *Cymothoa falcata* Fabricius, 1787 but the identity of that species is not known. *Nerocila blainvillii* is apparently an unjustified replacement name for *N. falcata* (G.C.B. Poore and H. Lew Ton, in litt.). Leach's material is held at the British Museum (BMNH 1979: 400:2), but has never been fully described. Material currently being identified as *Nerocila bivittata* (Risso, 1816) (see Trilles, 1975b) appears conspecific with *N. blainvillii.*

Remarks. *Nerocila* is readily identified by the anterior margin of the cephalon lacking a rostrum, posterior margin of cephalon strongly trilobed, large coxae that are usually conspicuous in dorsal view, ventrolateral processes on pleonites 1 and 2, and uropods that always project well beyond the posterior of the pleotelson. *Creniola* is separated by lacking large ventrolateral extensions on pleonites 1 and 2, uropods that do not project beyond the pleotelson, and coxal plates not visible in dorsal view.

Up to this work about 62 species of *Nerocila* had been named. With the synonymies listed here, and with those species placed into *nomen dubium* and *nomen nudum,* this total is reduced to 28 species. Of these 28 species a further eight have to be considered of doubtful validity because of poor description, lack of types, or probability that they are junior synonyms. A list of all *Nerocila* species is given, with comments on their current status.

Bowman (1978) revived *Emphylia* Koelbel, 1879, as a subgenus of *Nerocila.* The usefulness of subgenera within the family is questionable, and could lead to yet further complexity of synonymies. The subgenus is not clearly separated from *Nerocila* as some of the characters utilised intergrade. Initially, the antennule bases being set close together prompted Koelbel (1879) to establish a genus for the species *Emphylia ctenophora.* This was later found to be a synonym of *Nerocila sundaica* and redescribed by Bowman (1978), who recognised *Emphylia* as a subgenus. This character no longer seems to be useful as two species that belong to the *Emphylia* group, *Nerocila sigani* and *N. monodi,* have antennule bases set clearly apart. Considering the major characters that currently separate the genera *Anilocra, Creniola, Pleopodias, Renocila* and *Nerocila,* it can be seen that two suites of characters separate genera: mouthpart differences, and coxal and pleonal differences. *Emphylia* has an identical mouthpart, coxae and pleonal morphology to *Nerocila.*

I propose to recognise two species groups within *Nerocila,* to define them, but not to give them formal nomenclatural status. These are the *Nerocila* group and the *Emphylia* group. This will provide the same phyletic information as subgenera, but simplify citation and synomymies. I have two reasons for such action. Firstly, if these subgenera are maintained, it sets a precedent for creation of yet further subgenera within *Nerocila* (such as for *N. lomatia,* and for *N. excisa* and *N. trichiura),* and also in other cymothoid genera. In a family where genera provide problems in discrimination, and generic boundaries are not clearly established, the proliferation of subgenera is not to be encouraged. Secondly, omitting subgenera will simplify citation and non-specialists will not be confused by changes in subgeneric nomenclature and quadrinomials (e.g. *Nerocila (Nerocila) acuminata* f. *aster* in Brusca, 1981).

Key to Australian Species of *Nerocila*

1. Coxae 5—7 posteriorly rounded, shorter than respective segment. ..... *N. lomatia* n. sp.
——Coxae 5—7 posteriorly acute, as long or longer than respective segment. 2
2. Pereopod 7 manifestly longer than 6; uropod endopod with serrate margin(s) (*Emphylia* group). 3
——Pereopod 7 subequal in length to 6; uropodal rami not serrate (*Nerocila* group). 4
3. Both margins of uropod endopod serrate. ..... *N. monodi*
——Only lateral margin of uropod endopod serrate. ..... *N. serra*
4. Pleonites 1 and 2 with ventrolateral processes very large, laterally directed; anterior margins convex. ..... *N. congener*
——Pleonites 1 and 2 ventrolateral process narrow, posterolaterally directed; anterior margins straight or weakly convex. 5
5. Uropod exopod straight, elongate about 8 times longer than proximal width. ..... *N. phaiopleura*
——Uropod exopod curved, less than 3.5 times longer than proximal width. 6

6. Uropod exopod about twice as long as endopod; endopod distal margin deeply indented. ..... *Nerocila* sp.

——Uropod exopod slightly longer (1.2—1.5) than endopod; distal margin not deeply indented. 7

7. Uropod endopod lateral and medial margin subparallel; distal margin obliquely truncate, with distomedial tooth. ..... *N. orbignyi*

——Uropod endopod lateral and medial margins diverging; distal margin concave, without prominent distomedial tooth. ..... *N. barramundae*

Nerocila Group

Diagnosis of female. Antennule and antenna basal articles widely separate; cephalon anterior margin strongly produced; pereopods 1—6 without spines; pereopod 7 subequal to, or slightly longer than 6, feebly spinose or without spines.

Remarks. Included are all species currently placed in the genus except for those placed in the *Emphylia* group. *Nerocila trichiura, Nerocila exocoeti, Nerocila exisa* and *N. lomatia* form a group of species characterised by short, weakly acute or posteriorly rounded coxae, not having the posterolateral angles of the pereonites produced, and having small ventrolateral processes on pleonite 1 and 2. *Nerocila lomatia* is the only species of the genus which has the posterior coxae shorter than the respective pereonite, and the species should at present, be regarded as *incerta sedis.*

Emphylia Group

Diagnosis of female. Antennule and antenna basal articles set closer together than *Nerocila* group, or in contact; anterior margin of cephalon not strongly produced; pereopods 3, 6 and 7, or 6 and 7 with prominent spines; pereopod 7 manifestly longer than pereopod 6.

Remarks. The only Australian representatives are *Nerocila monodi* and *N. serra.* Other species are *Nerocila sundaica* Bleeker, *Nerocila arres* Bowman & Tareen, *Nerocila kisra* Bowman & Tareen, *Nerocila sigani* Bowman & Tareen, *Nerocila longispina* Miers, and *Nerocila serra* Schiödte & Meinert.

Nerocila sp.

Fig. 5

Material examined. Female (ovig 15.5), NNW of Port Hedland, WA, 18°53′S, 117°47′E, 20 May 1978, depth 135—138m, coll. B. Hutchings on *Courageous* (WAM 604-85).

Remarks. The uropod morphology of this specimen is unique. Comparison with illustrations of *Nerocila* species and to types of most Indo-Pacific *Nerocila* species resulted in the conclusion that the specimen represents a new species. It shows some similarity to *Nerocila phaiopleura* but differs in having the posterolateral margins of pereonites 5—7 produced, and distinct uropod and pereopod morphology.

Several species of *Nerocila* have widely variable morphologies (e.g. *Nerocila acuminata,* see Brusca, 1981; *Nerocila sundaica,* see Bowman, 1978; *Nerocila orbignyi).* Other species present a far more uniform appearance (e.g. *Nerocila monodi,* the related *Creniola saurida, Creniola laticauda).* A single specimen gives no indication of the potential variation, and establishing a species on a single specimen would be imprudent.

Figures are given here to enable new material to be identified when encountered.

Nerocila barramundae n. sp.

Figs 6, 7

Material examined. HOLOTYPE, female (ovig 31.0), Broad Sound, Rockhampton, Apr 1981. on dorsal fin of *Lates calcarifer,* coll. J. Peady (QM W11008). PARATYPE, female (ovig 29.0), Karumba, Queensland, ca. 1982, on base of pelvic fin of *Lobotes surinamensis,* coll. E. Grant (QM W10257).

Type locality. Broad Sound, Rockhampton, Queensland.

Description of female. Body 2.3—2.6 times as long as wide. Cephalon anterior margin subquatrate to rounded; eyes with facets idistinctnct. Posterolateral margins of pereonites not produced; coxae 3 and 4 with posterior margins truncate, coxae 4—7 becoming progressively more acute, not extending beyond posterior of respective segments. Pleonites 1 and 2 with ventrolateral process posteriorly directed; lateral margins of pleonites 3—5 not extended; pleonite 5 about 0.73 width of pereonite 6. Pleotelson about as long as wide, posterior margin broad.

Antennules separated by slightly more than width of article 1 (0.25 width of cephalon); antenna with setae on posterior margin of article 4.

Mandible palp article 3 with long setae on distolateral margin. Maxilliped article 3 with 2 small and 3 prominent spines.

Pereopod 1 with large, smoothly curved, very robust dactylus; pereopods 2—4 with dactylus increasing in length; decreasing in length from 5—7;

pereopod 7 with small spines along posterior margin of merus, carpus and propodus.

Pleopod 2 appendix masculina about 0.5 length of endopod. Pleopods 3 and 4 endopod with single lobe, proximomedial lobe slightly folded. Pleopod 5 endopod with 2 large folded lobes.

Uropod exopod slightly longer (1.16) than endopod, straight, margins converging to narrowly rounded point; endopod with medial margin convex, distal margin subtruncate or concave; distomedial angle of peduncle bluntly rounded.

Male. Not known.

Colour. Dark grey, with pale clear band along posterior of pereonites.

Size. Up to 31.0 mm.

Remarks. The combination of short subtruncate uropodal endopod, with short coxae and lack of posterolateral pereonal processes serves to distinguish *N. barramundae* from others of the genus. Other characters to note are the large stout pereopod dactylus on all pereopods, the short pleotelson and the ventrolateral process of pleonites 1 and 2 being posteriorly directed.

Southwell (1915) described *Rocinela latis,* parasitic on *Lates calcarifer,* near Calcutta. This species appears to be a juvenile *Nerocila.* At present males and juveniles of many cymothoid genera (e.g. *Mothocya* — Bruce, 1986; *Anilocra* — Williams & Williams, 1981, Bruce, 1987a, and discussion for *Nerocila orbignyi)* are not possible to identify to species level unless they are associated with an adult female. As the whereabouts of the types of *N. latis* is not known, and their identity is obscure, I regard it as *species inquirenda.* Rather than risk incorrect usage of that name, the adult specimens from Australia are described as a new species.

Hosts. *Lates calcarifer* and *Lobotes surinamensis,* both euryhaline fishes.

Distribution. Karumba, Gulf of Carpentaria and Broad Sound, Rockhampton, Queensland.

Etymology. The epithet is derived from barramundi, the Aboriginal name for *Lates calcarifer.*

Nerocila congener Miers

Figs 8, 9

Nerocila congener White, 1847: 108, nomen nudum.
Nerocila congener Miers, 1880: 468.—Nierstrasz, 1931: 125; Ellis, 1981: 124.

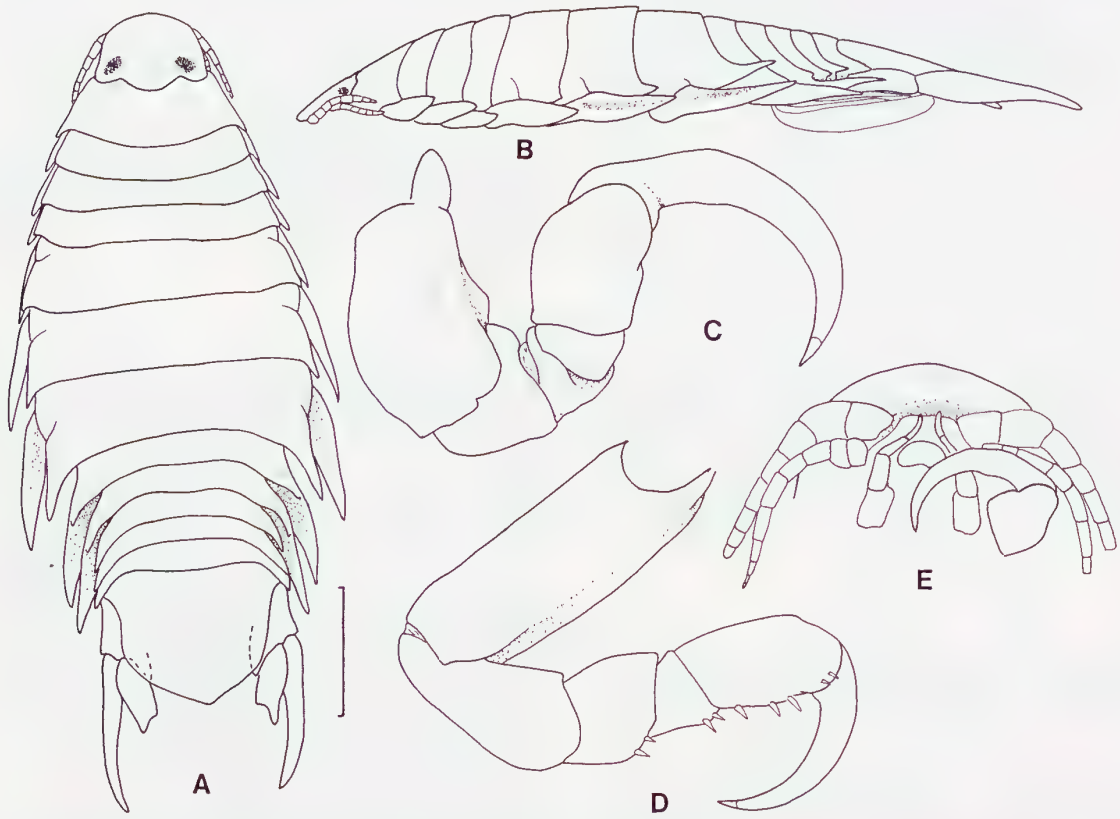

Fig. 5. *Nerocila sp.,* WAM 604-85. **A,** dorsal view; **B,** lateral view; **C,** pereopod 1; **D,** pereopod 7; **E,** buccal area. Scale line 3.0 mm.

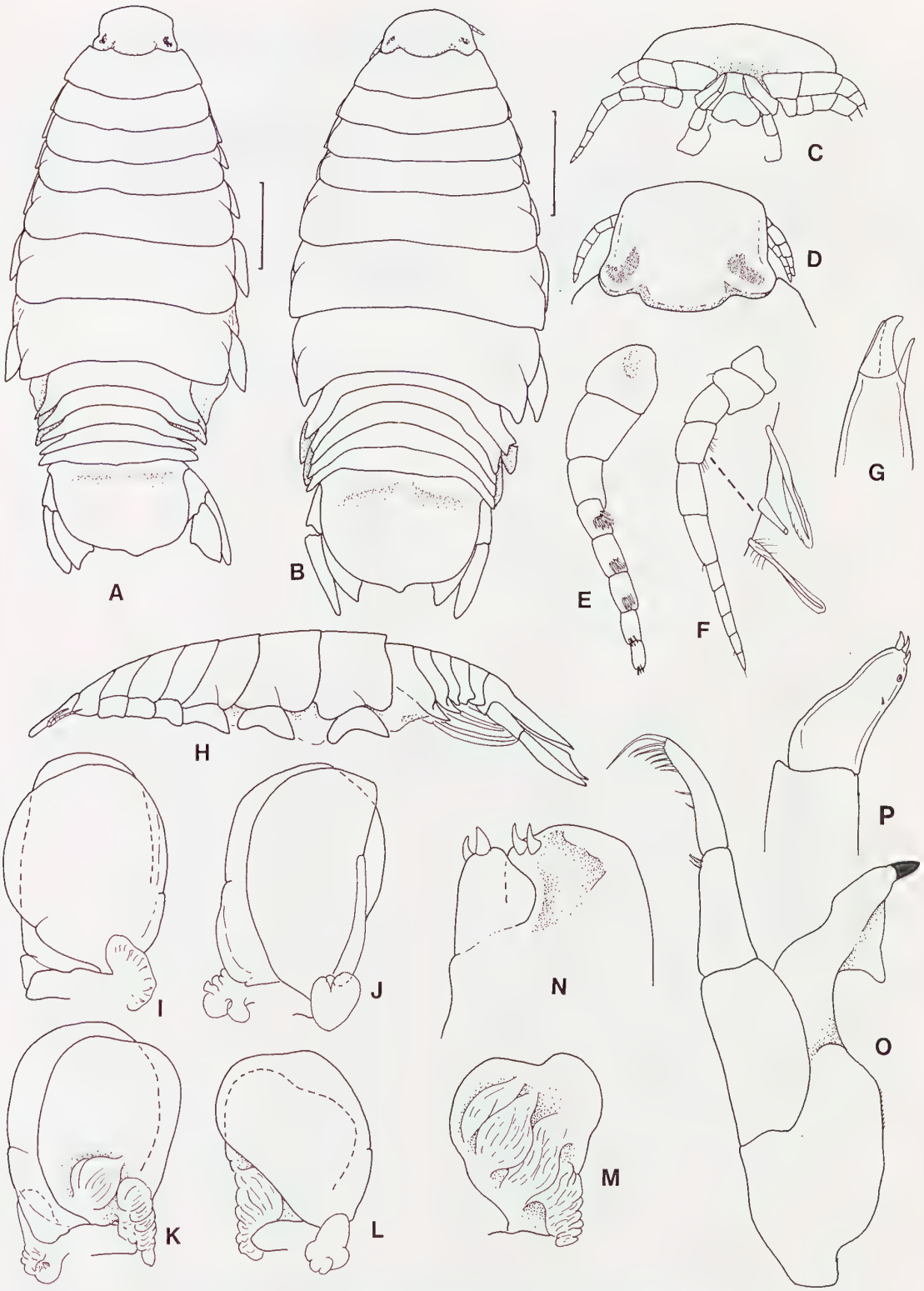

Fig. 6. *Nerocila barramundae* n. sp. Figs A, C, D, H, holotype, remainder paratype. **A,** dorsal view; **B,** dorsal view; **C,** frons; **D,** cephalon, dorsal view; **E,** antennule; **F,** antenna; **G,** maxillule apex; **H,** lateral view; **I—L,** pleopods 1—3, 5; **M,** pleopod 5, posterior view; **N,** maxilla apex; **O,** mandible; **P,** maxilliped article 3. Scale line 5.0 mm.

Nerocila Cebuana Schiödte & Meinert, 1881: 11, pl. 1, figs 4, 5.
Nerocila philippinensis Bovallius, 1887: 3, pl. 1, figs 1—12.—Nierstrasz, 1931: 125.
Nerocila cebuana.—Nierstrasz, 1931: 125.
Not *Nerocila cebuana.*—Nierstrasz, 1915: 73 (= *Nerocila* sp.?).

Material examined. HOLOTYPE, female (ca. 28.0). Philippine Islands, (No. 637a), coll. Mr. Cumming (BMNH 1979:337.1). Female (ovig 28.5), Arafura Sea, N.T., 11°26′S, 133°09′E, 16 Nov 1980, 30 m depth, trawl (AM P37155).

Types. The holotype is held at the British Museum (Natural History). I was not able to locate type specimens of *N. cebuana* or *N. philippinensis.*

Type locality. Philippines (Miers, 1880).

Description of female. Body to 2.6—2.8 times as long as wide. Cephalon anterior margin wide; eyes with facets indistinct. Posterolateral angles of pereonites 1—6 not produced, those of pereonite 7 weakly so. Coxa 2 with posterior margins rounded, coxae 3—7 becoming progressively more acute towards posterior; those of pereonites 6 and 7 extending slightly posterior to their respective segments.

Fig. 7. *Nerocila barramundae* n. sp. G, holotype, remainder paratype. **A—E,** pereopods 1, 2, 4, 6, 7; **F,** uropod; **G,** uropod.

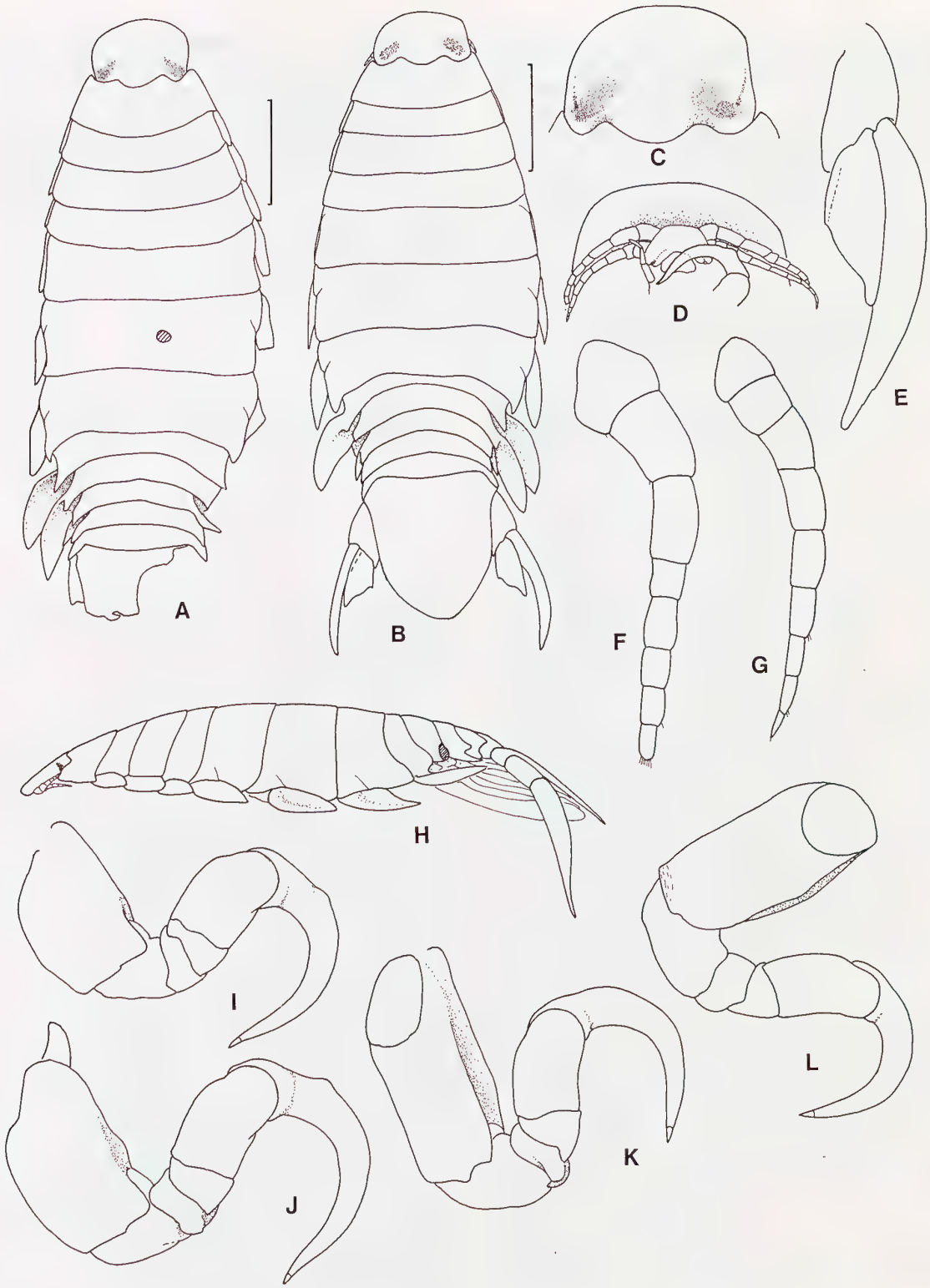

Fig. 8. *Nerocila congener.* All female, NWS, AM P37155, except A. **A,** holotype; **B,** dorsal view; **C,** cephalon; **D,** frons; **E,** uropod; **F,** antennule; **G,** antenna; **H,** lateral view; **I–L,** pereopods 1, 2, 6, 7 respectively. Scale lines 5.0 mm.

Pleonites 1 and 2 with ventrolateral processes greatly expanded, extending laterally to width of pereon; pleonites 3—5 lateral margins not strongly produced; pleonite 5 about 0.6 width of pereonite 6. Pleotelson about 1.2 times as long as wide, linguiform, margins of posterior half thin.

Antennule bases separated by length of peduncular articles 1 and 2. Mandible palp article 3 with short spatulate setae on distolateral margin. Maxilliped article 3 with 2 curved spines.

Pereopod 1 dactylus with nodule on anterior margin; dactylus apex reflexed outwards. Pereopod 2 similar to 1, but basis longer; pereopods 5—7 with shorter dactylus, without nodule.

Pleopods 3 and 4 with endopod lobes moderately developed; those of pleopod 5 highly developed. Uropod exopod twice as long as endopod, curving smoothly to narrow apex; endopod with narrow distolateral projection, sinuate posterior margin.

Male. Not known.

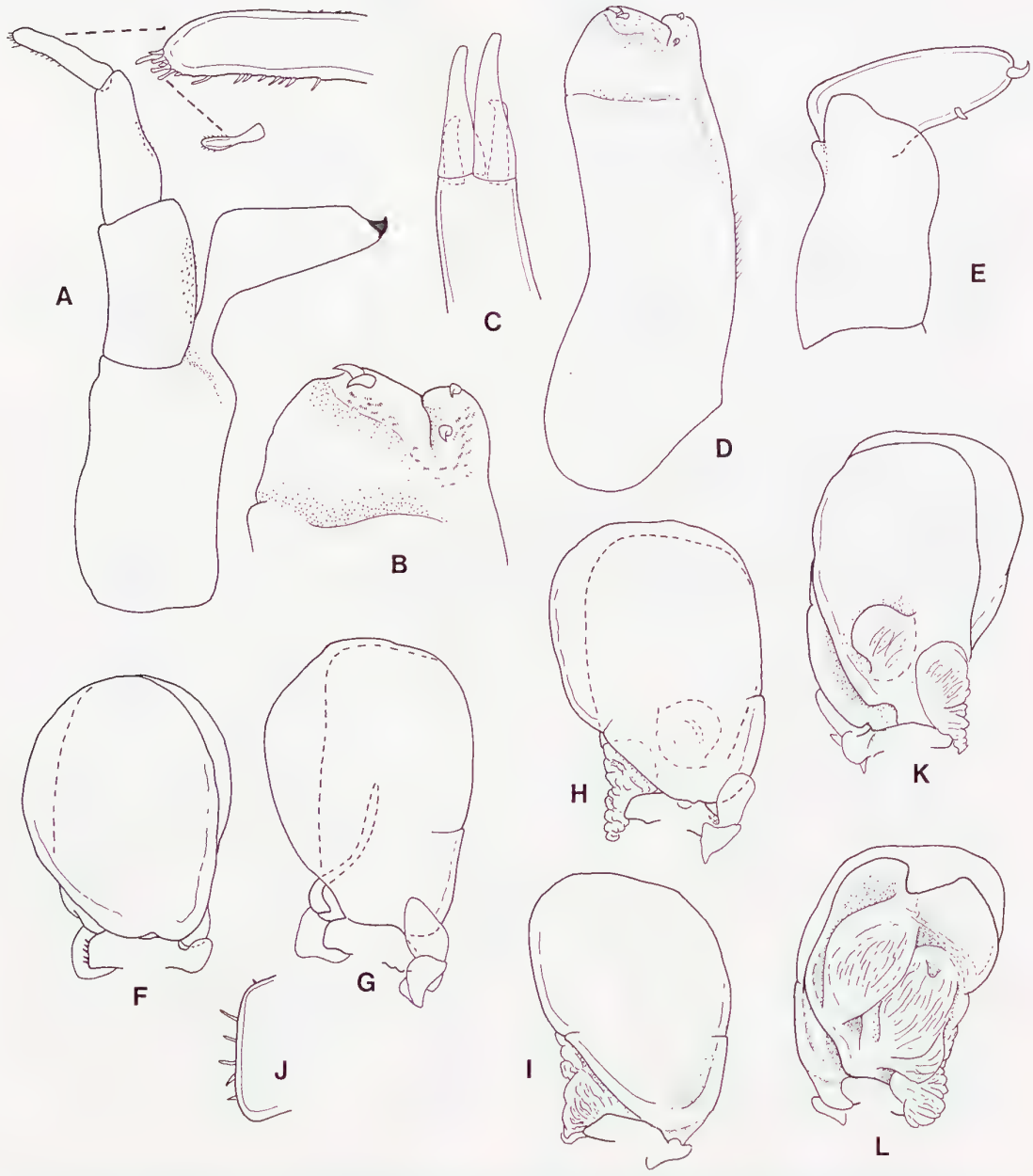

Fig. 9. *Nerocila congener.* All female, NWS, AM P37155. **A,** mandible; **B,** maxilla apex; **C,** maxillule apex; **D,** maxilla; **E,** maxilliped articles 2 and 3; **F—I,** pleopods 1—3, 5 respectively; **J,** pleopod 1, peduncle medial margin; **K,** pleopod 3, posterior view; **L,** pleopod 5, posterior view.

Colour. Pale tan in alcohol.

Size. Up to 28.5 mm.

Remarks. This distinctive species is easily recognised by the relatively narrow body, lack of posterolateral extensions to the pereonites, broad cephalon, very large and broad ventrolateral processes on pleonites 1 and 2, and the uropod morphology.

Although I was not able to examine the type specimens of *Nerocila cebuana* and *Nerocila philippensis* the illustrations given by Schiödte & Meinert (1881) and Bovallius (1887) readily allow their species to be recognised as synonyms of *Nerocila congener.*

Hosts. Not known.

Distribution. Northern Australia; previous records are Philippines (Miers, 1880; Bovallius, 1887), Cebu Island, Philippines (Schiödte & Meinert, 1881).

Nerocila lomatia n. sp.

Figs 10, 11

Material examined. HOLOTYPE, female (ovig 16.0), 4 km north of Jones' Shoal, Cobourg Peninsula, NT, 10°53′S, 132°14′E, 12 Sept 1975, coll. M.V. *Gemeni* (NTM Cr2302). PARATYPES: 3 females (ovig 8.5, 8.5, 8.5, 7.0), King Creek, Shoal Bay, NT, 12°21′S, 131°00.5′E, 11 Dec 1974, salinity 23.3‰, coll. N.T. Fisheries Division (NTM Cr773). Female (ovig 11.0), Cameron's Beach, Darwin, NT, 12°21′S, 131°00′E, 14 Aug 1975, salinity 35.3‰, coll. NT Fisheries Division (NTM Cr772). Female (ovig 10.0), AIMS Harbour, Cape Ferguson, Queensland, 4 Feb 1979 on gills of *Pellona ditchella,* coll. AIMS—AM (AM P37258). Female (ovig 9.0), Serpentine Creek, Brisbane, Qld, 17 Feb 1975, on *Mugil georgii,* coll. R. Harrison (QM W4823). Male (6.5), Redland Bay, Moreton Bay, Qld, 6 Mar 1973, coll. CSIRO (WAM 609-85). Female (ovig 7.5), Deception Bay, Moreton Bay, Qld, no date, coll. CSIRO (WAM 610-85).

Type locality. Off Cobourg Peninsula, N.T., Australia, 10°53′S 132°14′E.

Description of female. Body about twice as long as wide. Cephalon anterior margin subtruncate, gently convex; eyes prominent, occupying 0.4 width of cephalon. Pereonite posterolateral margins not produced, rounded; coxae 2—4 as long as segment; coxae 5—7 shorter than segment; with posterior margins broadly rounded. Pleon slightly skew to pereon, about 0.5 width of pereon; pleonites 1 and 2 with ventrolateral processes posteriorly directed, weakly produced; lateral margins of pleonites 3—5 rounded, not produced. Pleotelson shield shaped, lateral margins curving to medial point.

Antennule extending to pereonite 1; antenna with 10 articles slightly longer than antennule.

Mandible palp articles 2 and 3 subequal in length; article 3 without setae. Maxilliped article 3 with 2 large terminal spines and small midlateral spine.

Pereopods without spines, dactylus without nodules; pereopod 1 dactylus about 2.0 times longer than propodus; that of pereopod 2 about 2.3, and pereopod 7 about 1.9.

Pleopod 1 endopod proximomedial lobe small. Pleopod 2 appendix masculina about 0.5 length of endopod. Pleopods 3 and 4 with single small fold on endopod. Pleopod 5 with 2 large folds. Uropod exopod tapering evenly to rounded apex, about 1.6 times longer than endopod.

Male. About 2.7 times as long as wide; pleon about 0.6 width of pereon. Appendages similar to those of female, but maxilliped article 3 with larger spines, mandible palp with 2 terminal setae, and pereopod 7 with 5 small spines on propodal palm, 3 small spines on posterior margin of merus.

Colour. Present material pale tan or brick red, with chromatophores along posterior of pereon and pleon segments, and lateral margin of uropod peduncle.

Size. Ovigerous females 7.0—16.0 mm (average 9.6 mm).

Variation. All specimens present a constant appearance; the degree that the pleon is twisted in relation to the pereon varies. The uropod exopod varies from 1.5—2.0 times longer than the endopod.

Remarks. This species is very similar to *Nerocila excisa* Richardson. Richardson's figures (1901, 1914) do not allow for comparison. Trilles (1972) account is far more detailed but does not give enough detail of the adult female. Examination of the type specimen of *Nerocila excisa* Richardson, 1914 (not *Aegathoa excisa* Richardson, 1901) shows that the coxae of the two species differ, with those of *N. lomatia* being much shorter and rounded posteriorly. Additionally the two species mature at different size ranges: *Nerocila excisa* females measure 17—20 mm while the Australian females measure 7—16 mm. The two species also occupy different habitats: *Nerocila excisa* is pelagic and oceanic (Brusca, 1981; Trilles, 1972) while *Nerocila lomatia* is estuarine and inshore. *Nerocila lomatia* is the first species of the genus to be recorded as a branchial parasite.

Nerocila lomatia forms one of the group of *Nerocila* species characterised by having the posterolateral margin of the posterior pereonites very weakly, or not all produced, short coxae, short ventrolateral extensions of pleonites 1 and 2, and elongate uropodal rami. The other species of this group are *Nerocila trichiura, Nerocila exocoeti* and *Nerocila excisa. Nerocila lomatia* differs from these species by its posteriorly rounded coxae and dorsoventrally flattened body shape. Its position within the genus is regarded as *incerta sedis.*

Distribution. Northern Territory, and Moreton Bay, Queensland; in estuarine waters with recorded salinities of 23.3 and 35.3‰.

Hosts. *Mugil georgii* and from the branchial chamber of *Pellona ditchella.*

Etymology. The epithet is derived from the Greek

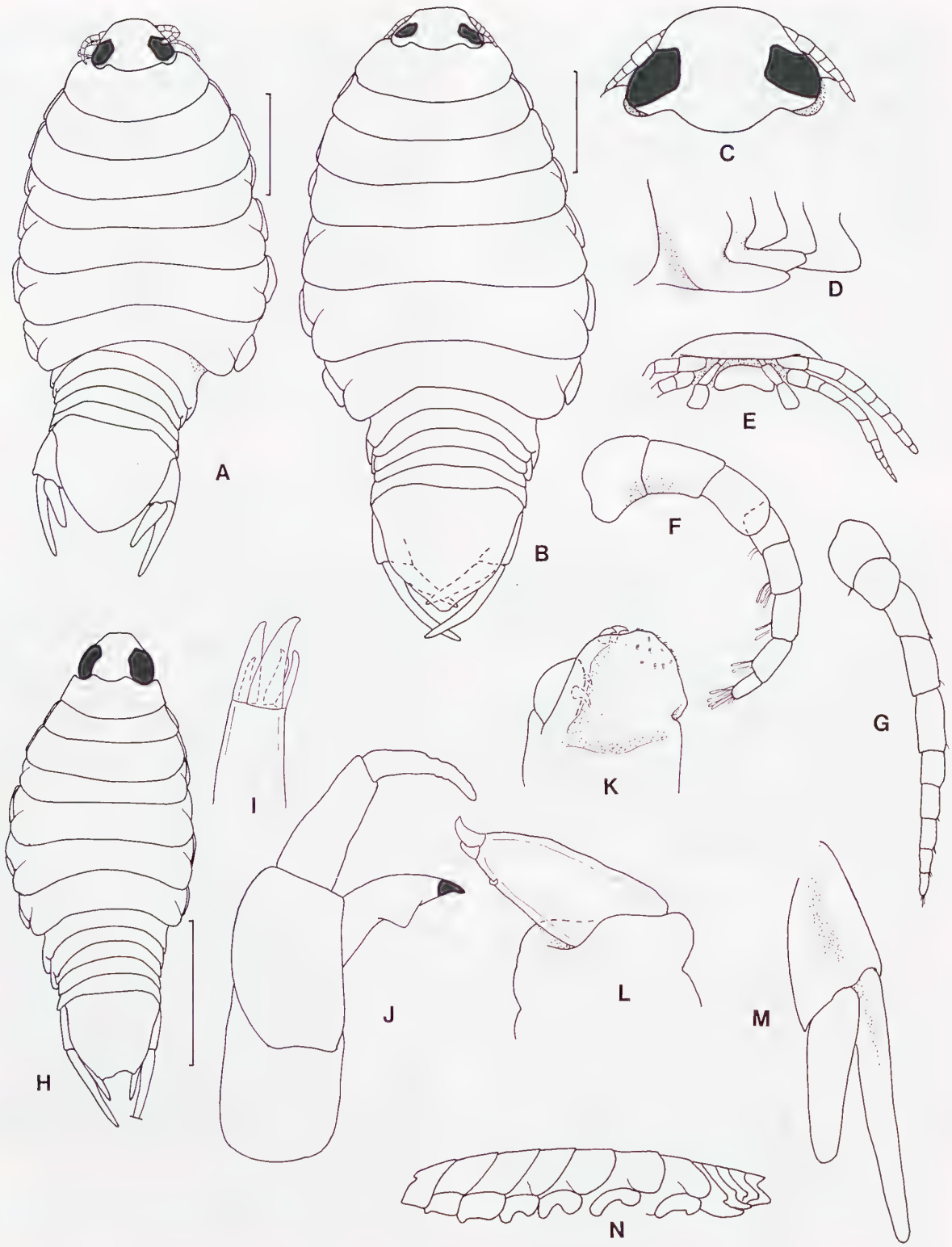

Fig. 10. *Nerocila lomatia* n. sp. B—E, holotype, H, female QM W4823, remainder paratype NTM Cr772. **A,** dorsal view; **B,** dorsal view; **C,** cephalon; **D,** pleon, lateral view; **E,** frons; **F,** antennule; **G,** antenna; **H,** dorsal view; **I,** maxillule apex; **J,** mandible; **K,** maxilla apex; **L,** maxilliped article 3; **M,** uropod; **N,** pereon and pleon. Scale lines 3.0 mm.

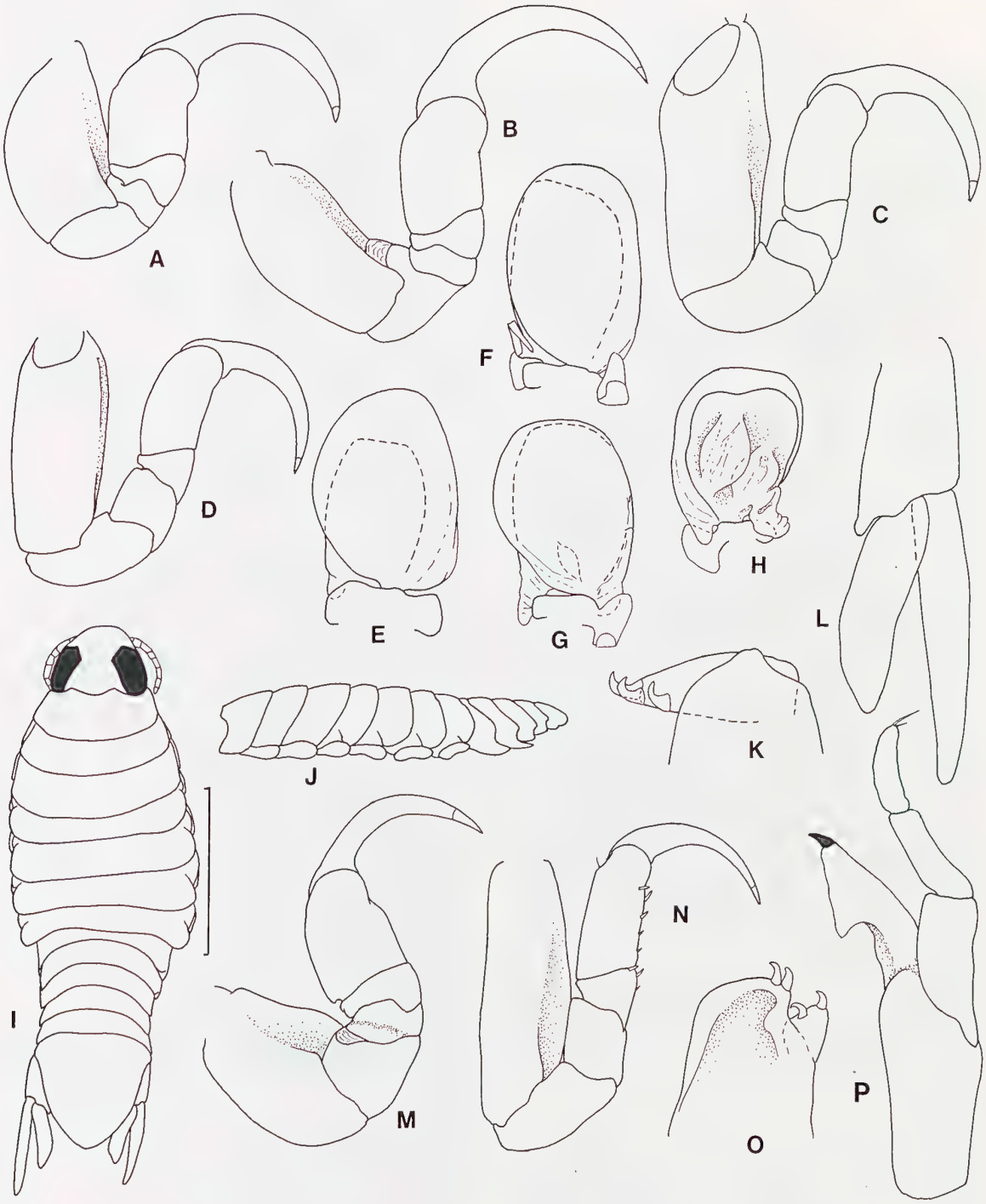

Fig. 11. *Nerocila lomatia* n. sp. A—H, female paratype NTM Cr772; I—P, male paratype WAM 609-85. **A—D,** pereopods 1, 2, 6, 7; **E—G,** pleopods 1, 2, 4; **H,** pleopod 5; posterior view; **I,** dorsal view; **J,** pereon and pleon, lateral view; **K,** maxilliped article 3; **L,** uropod; **M,** pereopod 1; **N,** pereopod 7; **O,** maxilla apex; **P,** mandible. Scale line 2.0 mm.

word *lomatia,* meaning border or coast and alludes to the species' distribution.

Nerocila orbignyi (Guérin-Méneville)
Figs 12—17

Ichthyophilus orbignyi Guérin-Méneville, 1832: 47.—1835, pl. 29, figs 3—3e.

Nerocila orbignyi.—Lucas, 1846: 76; Carus, 1885: 440; Nierstrasz, 1915: 73; Monod, 1931: 10, figs 5—11; Barnard, 1940: 403; Hale, 1940: 301; Dollfus, 1946: 73; Brian & Dartevelle, 1949: 140, fig. 122; Hurley, 1961: 268, 284; Trilles, 1962: 102, figs 6, 7; 1963: 609; 1964a: 5989; 1964b: 6545; 1964c: 2, 4; 1964d: 109; 1964e: 365, 367; 1964f: 128; 1968: 103, photo. 22—24, pls 30—34; 1969: 434; 1973b: 1271, figs 5—10, 15; 1975b: 363, figs 157—206, pl. 1, figs 4, 5; 1977: 14; 1986: 621; Wunder, 1962: 140, photo. 1—12; Scott, 1964: 23; Berner, 1969: 93; Day, Field & Penrith, 1970: 48; Mann, 1970: 188; Hewitt & Hine, 1972: 79, 100, 108; Lincoln, 1971, photo. 2, opp. p. 186; Trilles & Raibut, 1971: 81; 1973: 279; Romestand, Trilles & Lagarrigue, 1971: 447; Fryer & Iles, 1972: 257; Reichenbach-Klinke, Heinz-Hermann & Landott, 1973: 321; Romestand & Trilles, 1975: 2171, pl. 1; Dollfus & Trilles, 1976: 827; Romestand, Janicot & Trilles, 1977: 172; Kensley, 1978: 81, fig. 33C; Moreira & Sadowsky, 1978: 100, 110, 117; Romestand, 1979: 425, pl. 1, fig. 7; Thuet & Romestand, 1981: 33; O'Riordan, 1982: 551; Bragoni, Romestand & Trilles, 1983: 594; Rockicki, 1984: 96, figs 23.

Nerocila maculata Milne Edwards, 1840: 253.—Heller, 1866: 740; Bullar, 1876: 118; Stalio, 1877: 233; Stossich, 1880: 223; Schiödte & Meinert, 1881: 50, pl. 3, figs 7—11; Gerstaecker, 1882: 255; Chevreux, 1884: 519; Carus, 1885: 440; Bonnier, 1887: 370; Bolivar, 1892: 132; Acloque, 1899: 19; Nierstrasz, 1915: 74; Gibert i Olivé, 1920: 86; Monod, 1923a: 86; 1923b: 15; Popov, 1933: 194; Montalenti, 1948: 75; Balcells, 1953: 550, fig 10; Trilles, 1962: 102; 1968: 158, photo. 19, 53, 56; 1975a: 326, pl. 3, fig. 22; 1975b: 367, figs 207—248, pl. 1, figs 6—9; 1977: 13; 1986: 621; Berner, 1969: 94; Lagarrigue & Trilles, 1969: 117, photo. 1; Romestand, Trilles & Lagarrigue, 1971: 447, fig. 2; Romestand & Trilles, 1975: 271, pl. 1; Dollfus & Trilles, 1976: 826; Huwae, 1977: 16, figs 23, 24B; Holthuis, 1978: 29, fig. 1b, pl. 1; Moreira & Sadowsky, 1978: 100, 110, 113; Romestand, 1979: 425, pl. 1, fig. 8; Rockicki, 1984: 92, figs 22, 52c.

Nerocila affinis Milne Edwards, 1840: 253.—Duvernoy & Lereboullet, 1841: 218, 221—224; Gerstaecker, 1882: 256; Chevreux, 1884: 519; Bolivar, 1892: 133; Carvalho, 1944: 8; Trilles, 1973b: 1270.

Cilonera MacLeayi White & Doubleday, 1843: 268, *nomen nudum.*

Nerocila Mac Leaii.—White, 1847: 108.

Nerocila vittata Lucas, 1846: 77, pl. 8, figs 2a—d.—Gerstaecker, 1882: 263.

Nerocila bivittata.—Van Beneden, 1861: 143; Pelseneer, 1886: 218; Preud'homme de Borre, 1886: lxxxiv; Gourret, 1907: 89; Euzet, 1949: 30; Montalenti, 1948: 72, figs 30, 31, pl. 8, figs 4, 6; Amar, 1951: 530; Balcells, 1953: 550.

Livoneca sciaenae Beneden, 1871: 32, nomen nudum.

Nerocila imbricata.—White, 1847: 108; Miers, 1876: 107.

Nerocila Australasiae Schiödte & Meinert, 1881: 35, pl. 6, figs 7, 8.—Gerstaecker, 1882: 262.

Nerocila Neapolitana Schiödte & Meinert, 1881: 41, pl. 2, figs 9, 16.—Gerstaecker, 1882: 256; Carus, 1885: 439.

Nerocila Adriatica Schiödte & Meinert, 1881: 45, pl. 3, figs 1—4.—Gerstaecker, 1882: 255; Carus, 1885: 440; Popov, 1933: 194; Montalenti, 1948: 75; Trilles, 1962: 102.

Nerocila Orbignyi.—Schiödte & Meinert, 1881: 55, pl. 5, figs 1—5; Montalenti, 1948: 75; Szidat, 1955: 217, fig. 7, pls 1a—f, 2, 7c.

Nerocila cephalotes Schiödte & Meinert, 1881: 60, pl. 4, figs 16, 18;—Gerstaecker, 1882: 259; Stebbing, 1902: 55; 1910: 423; Barnard, 1936: 165; Van Name, 1920: 43, 53, figs 6—9; Monod, 1924: 436, figs A, B, p. 437, C, D, p. 441; Szidat, 1955: 215; Dollfus & Trilles, 1976: 826 Trilles, 1975a: 327, pl. 3, fig. 24; 1977: 14; 1979: 250; 1986: 620; Bowman, 1978: 35; Rockicki, 1981: 88; 1984: 26, figs 5—8, 52a,b, 54—59.

Nerocila Novae-Zelandiae Schiödte & Meinert, 1881: 70, pl. 5, figs 10, 11.

Nerocila Novae Zelandiae.—Gerstaecker, 1882: 262.

Nerocila (Ichthyophilus) Orbignyi.—Gerstaecker, 1882: 257.

Nerocila macleayi Miers, 1884: 301.—Thomson & Chilton, 1886: 154; Thomson, 1889: 263.

Nerocila macleayii.—Chilton, 1891: 68, pl. 11; 1911: 568; Hutton, 1904: 263; Hale, 1926: 206, figs 1, 4, 5; 1929: fig. 256.

Nerocila trailli Filhol, 1885: 451.—Hutton, 1904: 263; Nierstrasz, 1931: 126.

Nerocila laticeps Bovallius, 1887: 10, pl. 2, figs 22—26, pl. 3, figs 27, 28.—Stebbing, 1922: 2; Trilles, 1986: 621, fig. 1A.

Nerocila neapolitana.—Tattersall, 1905: 85; Norman & Scott, 1906: 39; Zirwas, 1911: 106; Monod, 1923b: 87; Endre, 1931: 83; Popov, 1933: 194; Montalenti, 1948: 75; Anon, 1957: 195; Trilles, 1962: 102.

Nerocila rhabdota.—Barnard, 1914: 371.

Nerocila macleayi.—Nierstrasz, 1915: 75; 1931: 125; Dollfus, 1946: 73; Ellis, 1981: 124.

Nerocila armatus.—Stebbing, 1921: 23.

Rosca rogans Stebbing, 1924: 10, pl. 15.—Barnard, 1936: 165.

Nerocila armata.—Barnard, 1925: 390; Trilles, 1973c: 257, pl. 1, fig. 4.

Nerocila australasiae.—Hale, 1926: 208; Nierstrasz, 1931: 125.

Nerocila neapolatena.—Dudich, 1931: 18 (lapsus).

Nerocila novae zeelandiae.—Nierstrasz, 1931: 126 (lapsus?).

Nerocila orbigugi.—Popov, 1933: 194 (lapsus?).

Nerocila orbignyi maculata.—Schuurmans Steckhoven, 1936: 26, figs 19—22.

Nerocila orbignyi orbignyi.—Ringuelet, 1947: 95, figs 1—3, pl. 1.

Nerocila d'Orbignyi.—Szidat, 1956: 129, fig. 2a; Trilles, 1961: 689, pls 1—3.

Nerocila novae zelandiae.—Trilles, 1975a: 323, pl. 3, fig. 19.

Nerocila fluviatilis.—Trilles, 1975a: 331, pl. 3, fig. 26.

?Nerocila armata.—Trilles, 1977: 15.

Material examined. Female (non-ovig 28.0), Hobbarttown, Neue Hollande, coll. W. Robertson (holotype of *Nerocila australasiae,* MCZ 1139). Syntypes of

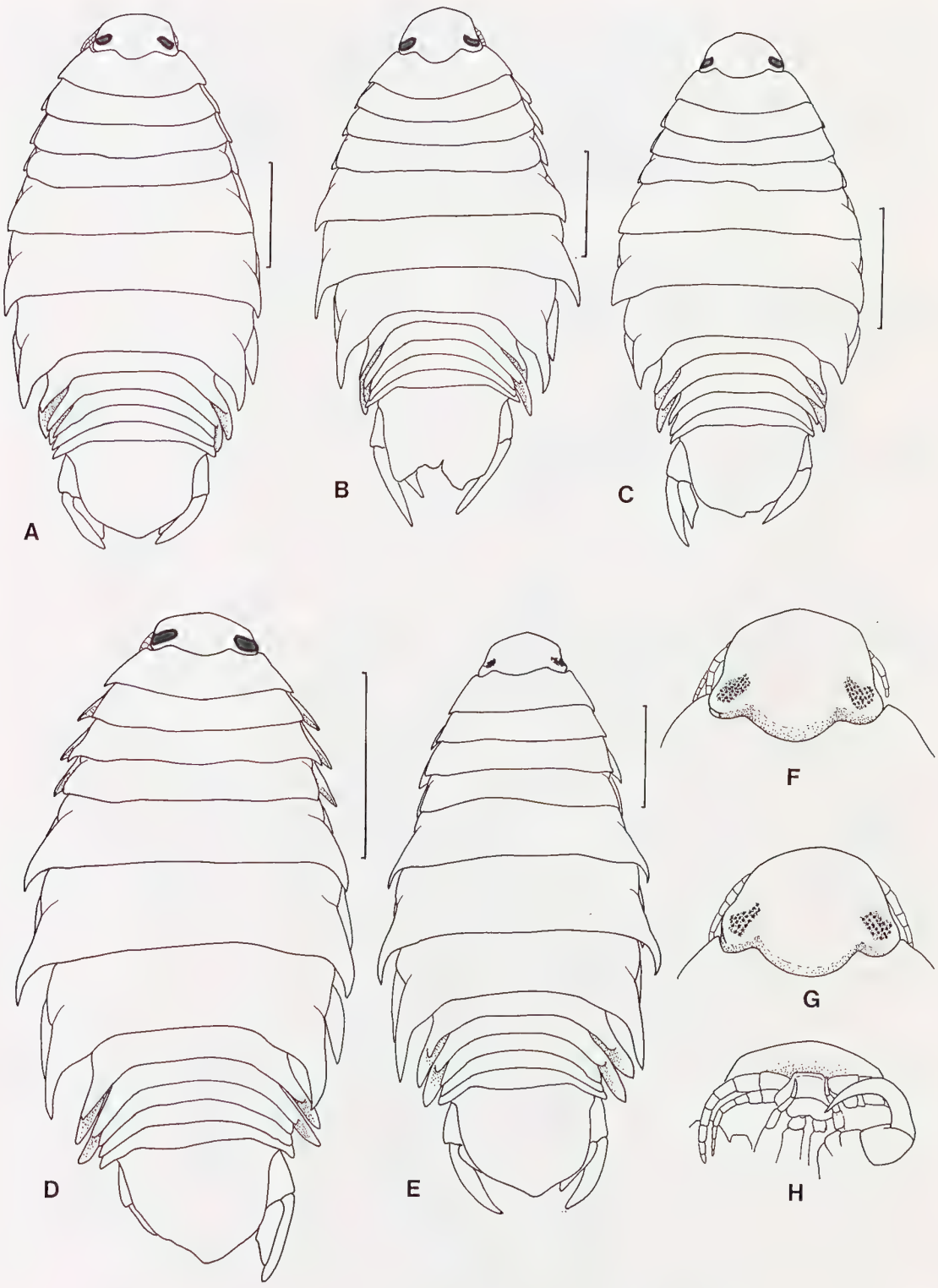

Fig. 12. *Nerocila orbignyi.* All from Walpole, WA (AM P37149), except where indicated. **A,** dorsal view, female #1; **B,** female #2; **C,** female #5; **D,** female #3; **E,** female, Mordialloc, Vic, NMV J11567; **F,** female #1, cephalon; **G,** female #5, cephalon; **H,** female #1, frons. Scale lines 5.0 mm.

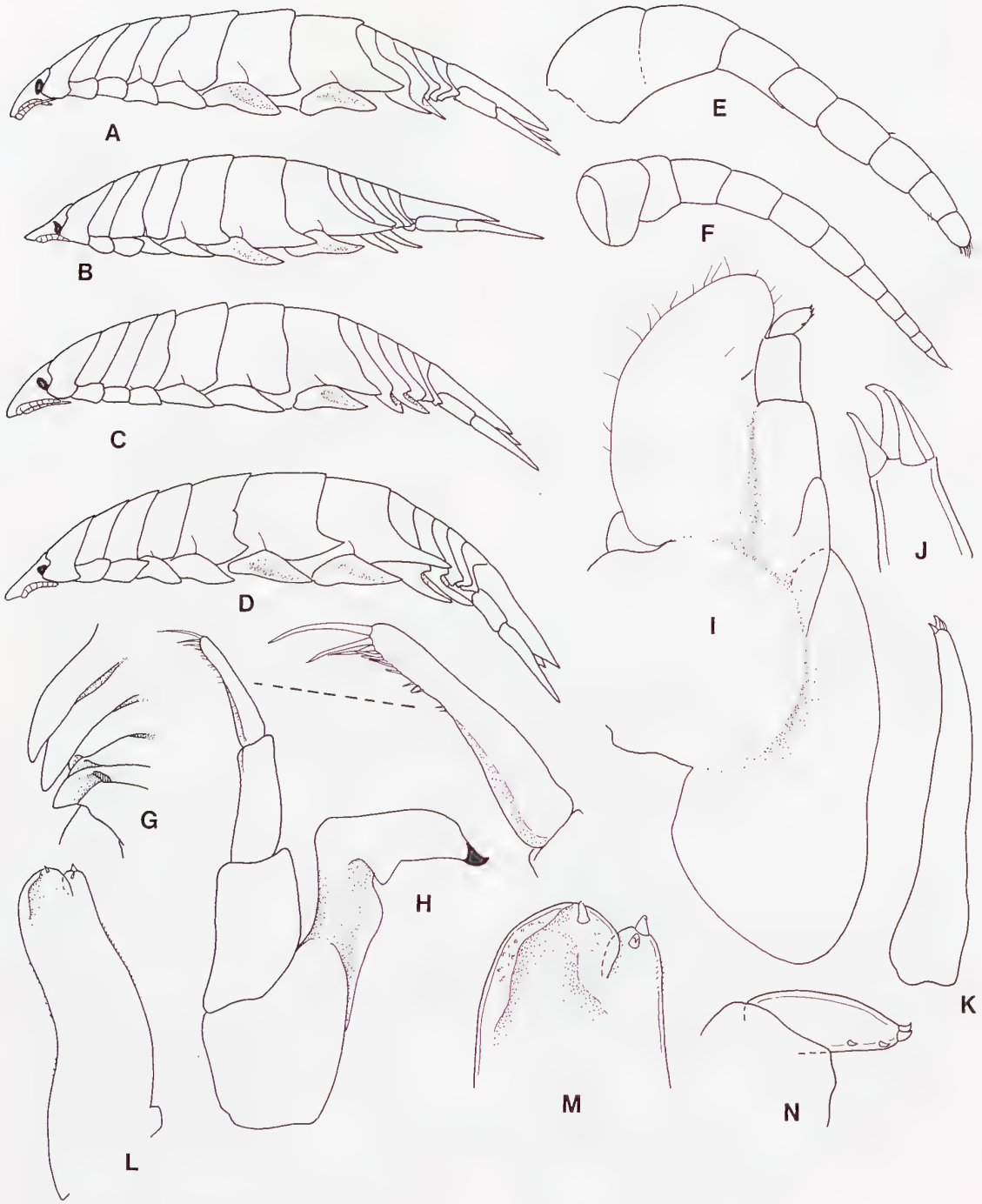

Fig. 13. *Nerocila orbignyi.* All female #1, Walpole, WA (AM P37149), except where indicated. **A,** lateral view; **B,** female #2; **C,** female #5; **D,** female, Mordialloc, Vic, NMV J11567; **E,** antennule; **F,** antenna; **G,** right pleonites, ventral view; **H,** mandible; **I,** maxilliped; **J,** maxillule apex; **K,** maxillule; **L,** maxilla; **M,** maxilla apex; **N,** maxilliped article 3.

Nerocila macleayii Miers: female (ovig 26.5), New Zealand, taken out of the mouth of a fish, coll. A. Sinclair (BMNH 1979:415:1); female (19.0, uropods missing), New Zealand, coll. A. Sinclair, No. 6366 (BMNH 1845:30); female (24.0) New Zealand, No. 211a (BMNH 1842:55); female (23.0) no data (BMNH 1979:414:1); female (ovig 24.5), Africa, No. 211a, W.E. Leach collection (BMNH 1979:417:1); male (12.5), west coast, America, coll. Capt. Kellett and Lieutenant Wood (BMNH 1850:12, = *N. acuminata).* Male (16.0), Nouvelle Zelande, Filhol 1832-75 (MNHN Is. 553, holotype of *Nerocila trailli).* Males (17.0, 15.5), Quoy et Gaimard, 918 (MNHN Is. 265) and male (NMW 5277), syntypes of *Nerocila novaezelandiae).* Also examined: holotype of *Nerocila japonica* (NRS Is. 4975, see Fig. 34G-J), holotype of *Nerocila maculata* (MNHN, Paris Is. 637, nothing but fragments and debris in tube), and holotype of *Nerocila falklandica* (female, non-ovig 21.0), taken on fish in Falkland Sound (BMNH 1985:266:1).

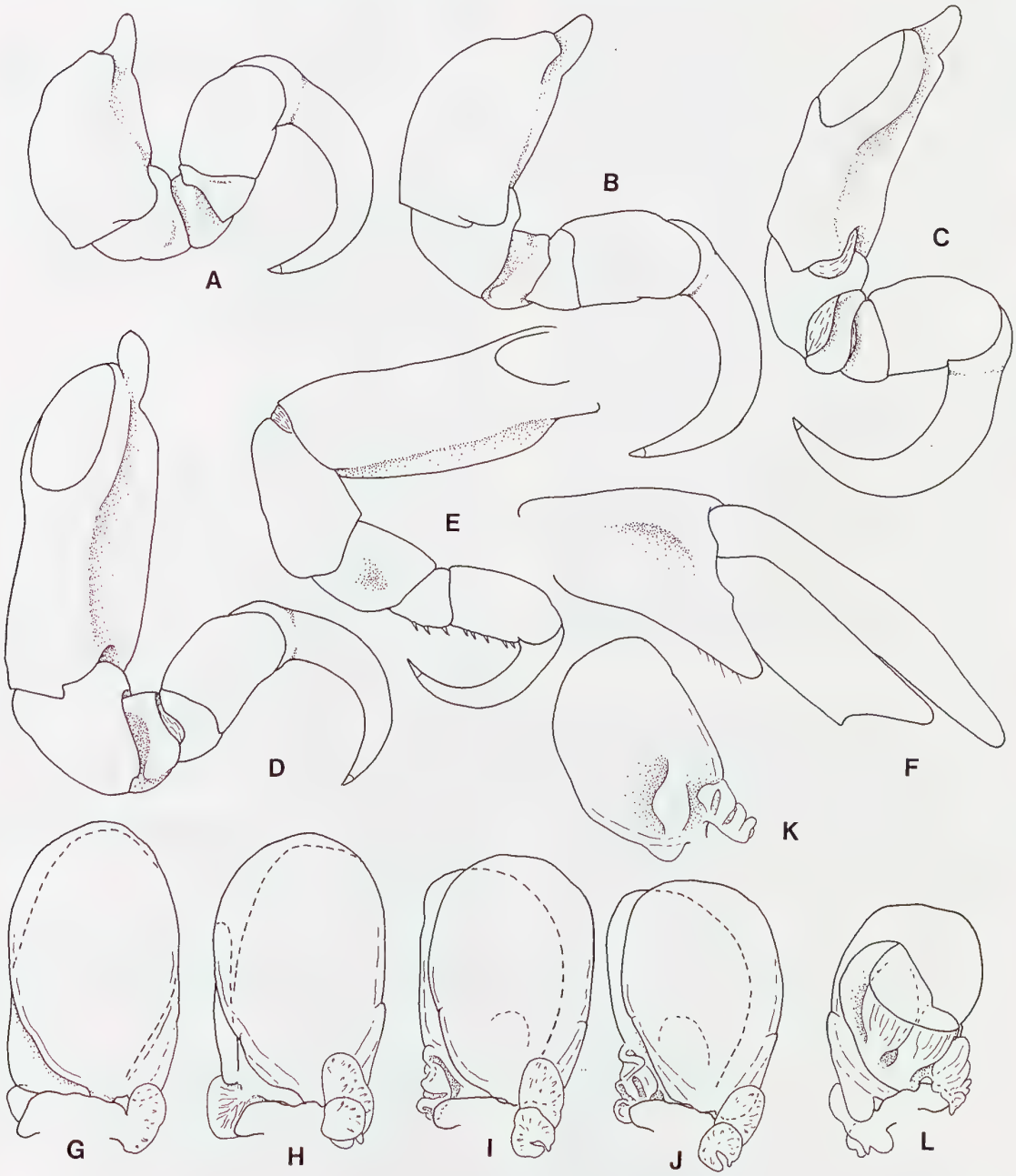

Fig. 14. *Nerocila orbignyi.* All female #1, Walpole, WA (AM P37149). **A–E,** pereopods 1, 2, 4, 6, 7 respectively; **F,** uropod; **G–J,** pleopods 1–4 respectively; **K,** pleopod 3, endopod, posterior view; **L,** pleopod 5, posterior view.

Non-type. Females (ovig 20.5), De Mak, Lightship *Texel,* Waddenzee, Netherlands, 22 Sep 1975, on *Crenimugil labrosus* (Risso), coll. C. Sweener (RMNH 5141). 2 females (ovig 18.0, 19.0), Golfe du Lyon, France, on fin of Mugilidae, no other data (identified by Trilles in 1975) (MNHN Is. 531). Females (ovig #1 31.0, 29.0, #2 27.5, 27.0), Bay of Naples, Italy, purchased by Dr. Dohrn, April 1882 (AM P37158). Female (ovig 30.5, from a series of 20 females, 1 male and 4 broken or dissected specimens), Naples, ca. 1956, donated by University College of London (BMNH unreg). Other RMNH numbers: 5471-5474 (Holland; Split, Jugoslavia); 5, 1324 (Middellandse Zee, Holland); 32 (Cadiz, Spain). Female (ovig 31.5), Bay of Eilat, Israel, 19 Oct 1962, on carangid, coll. Paperna (USNM acc. #305345). Female (24.0), Cap Blanc, Mauritania, West Africa, coll. Theo Monod (BMNH 1924.5.30.11-15). Female, Oamaru, New Zealand, leg. H. Suter (reported on by Nierstrasz, 1915 (RMNH 4). Female (ovig 26.0), west coast of South Island, New Zealand, between Butler and Grey Rivers, 29 Nov 1936, coll. Captain C.W. Osterfeld (AM P10821).

Australian specimens. New South Wales: female (ovig 30.0), Palm Beach, Broken Bay, Nov 1926, caudal peduncle of *Pagrosomus auritus,* coll. M. Ward (AM P8753). Female (26.0), Port Jackson, 11 Oct 1959, caudal peduncle of Luderick, coll. E. de Villa (AM P37150). Female (ovig 20.5), male intermoult (14.0), Wallega Lakes, 19 Dec 1981 on 'bream', coll. C. Keenan (QM W10269). 2 females (ovig ca. 25.0, non-ovig 23.0), Nadgee Beach, 24 Nov 1973, on black bream (AM P20254). Victoria: 2 females (ovig 26.5, 26.0), Mordialloc, Port Phillip Bay, 13 Dec 1979, from 'snapper', coll. Hans Tusreil (NMV J11567). 3 females (ovig 34.0, 33.5, 29.0), Bass Strait, 39°52.5′S, 144°48.0′E, 3 Feb 1981, trawled, 49 m, on *Callorhynchus milii* (NMV J11566). South Australia: female (ovig 21.0), Anxious Bay, 25 Feb 1981, 55 m, trawled, coll. P. Halsey (SAM C4067). Western Australia: 7 females (ovig 24.5 #1, 23.0 #2, 21.0 #4, 21.0, 20.0 #5, 17.0 #3, non-ovig 18.0), male (16.0), aegathoid (13.0), off Walpole, 3 Mar 1986, on pectoral or caudal fins of *Pseudocaranx dentex,* coll. A. William (AM P37149).

Additional material. New South Wales: 1. Old collection. 4 females, Port Jackson (AM P5622). 2 females, Port Hacking, 1907 (AM P4907). Female, Port Hacking, 13 Apr 1935, gill opening of *Pagrosoma,* coll. L. Abrahams (AM P10642). Female, Shoalhaven, coll. C. Hedley (AM P9596). Male, Eden, on fin of flying gurnard, coll. A. Cameron (AM P3940). Female, from sunfish (AM P9589).

2. Recent collection. 2 females, off Port Stephens, 22—23 Jan 1963, off stingray, 73—82 m, coll. J.C. Yaldwyn, D.J. McMichael (AM P37151). Female (ovig 24.5), southwest arm, Port Hacking, 13 Mar 1975, pectoral fin of mullet, coll. CSIRO (WAM 1250-85). Female (ovig 25.0), Little Jerusalem Bay, Hawkesbury River, 9 June 1986, on pectoral fin of *Pagrosomus auritus,* coll. S. Keable (AM P37152). Female, Tuross Head, 20 Sept 1974, off kyphosids, coll. D. Hoese, I. Briggs and N. Carrick (AM P37153). Victoria: female, Mornington, 7 Aug 1977, parasite on flathead, coll. John van Leeuwin (NMV J11568). 2 females, Black Rock, 6 Dec 1979, on flathead (NMV J11570). 2 females, 2 males, Victoria (SAM C288). Female, no data (NMV J11569). Female, Port Phillip, no data, coll. Miss J. Allen (AM P11425). Tasmania: female, Frederick Henry Bay, Storm Bay, 42°55′S, 147°37′E, 21 July 1973, on *Sillago bassensis,* coll. P. Last on *Allanwood* (AM P37260). Female, Storm Bay, 12 Dec 1977, on Red Gurnard, 59 m, coll. *Craigmin* (QM W11014). 3 females, Storm Bay (AM E5677). 2 females, Storm Bay, 16 July 1909, on elephant shark (AM E4848). Female, off Nutgrove Beach, Derwent Estuary, Hobart, 24 Jan 1977, on dorsal fin of *Callorhynchus milii,* coll. P. Last — CSIRO (AM P37259). 3 females, 1 aegathoid, Frederick Henry Bay, Storm Bay, 1984, body of *Callorhynchus milii,* coll. CSIRO (AM P37261). Female, off Tasmanian coast (AM E6745). South Australia: 3 females, 2 males, no data (SAM C4086). Female, Anxious Bay, 25 Feb 1981, 55 m, coll. P. Halsey (SAM C4087). Female, The Coorong, ca. 35°45′S, 139°13′E, 1982, on *Acanthopagus butcheri,* coll. T. Byrnes (AM P37159). Western Australia: 4 females, Albany, from Skipjack (WAM 589-86). 6 females, aegathoid, Albany, with #13410/13415, from skipjack (WAM 587-86). Female, male, Wilson Inlet, 35°00′S, 117°20′E, 7—15 July 1971, coll. R. Lenanton (WAM 600-85). 2 females, Frankland River, from sea trout and whiting (WAM 591-86). Female, Nornalup Inlet, on tail of skipjack (WAM 588-86). Male, Nornalup, on tail of *Pomatomus saltatrix* (WAM 47-36). Female, Broke Inlet, 34°56′S, 116°27′E, 20 Oct 1976, on fish (WAM 1261-85). Female, Fremantle, 7 Nov 1957, coll. R.P. McMillan (WAM 585-86). 2 females without data (WAM 337-30, 65-33).

Types. The whereabouts of the types of *Nerocila orbignyi* is unknown.

Type locality. Modon, Greece, 36°49′N, 21°42′E (Guérin-Méneville, 1832).

Description of female. Body about 2.0 times as long as wide. Cephalon anterior margin with indistinct medial point; eyes small, about 0.3 width of cephalon. Pereonites 1—4 posterolateral angles not produced; pereonites 4—7 or 5—7 posterolateral angles produced, acute. Coxae of pereonites 2—4 with posterior margins rounded, coxae of pereonites 5—7 with posterior margins acute. Pleonite 1 longest; ventrolateral margins of pleonites 1 and 2 posteriorly directed, extending to, or beyond pleonite 5; pleonites 3—5 lateral margins weakly produced, narrowly rounded. Pleotelson lateral margins angled, then converging to caudomedial point.

Antennule articles 1 and 2 partly fused; antenna with 11 articles.

Mandible palp article 1 longest, 2 and 3 subequal in length; article 3 with about 4 small and 6 long setae on distolateral margin. Maxilliped article 3 with 4 recurved spines.

Pereopod dactyli without nodules. Pereopod 1 dactylus robust, about 2.2 times as long as propodus. Pereopods 6 and 7 subequal in size, each with carina on mediolateral margin; pereopod 7 with 3 spines on posterior margin of carpus, 5 spines on propodal palm.

Pleopod 2 appendix masculina about 0.5 length of endopod; pleopod 5 endopod with 2 large folds. Uropod exopod curving medially, about 1.6 times as long as endopod; endopod straight, distal margin obliquely truncate, with distomedial point.

Male. About 2.4 times as long as wide; coxae and posterolateral margins of pereonites not as produced

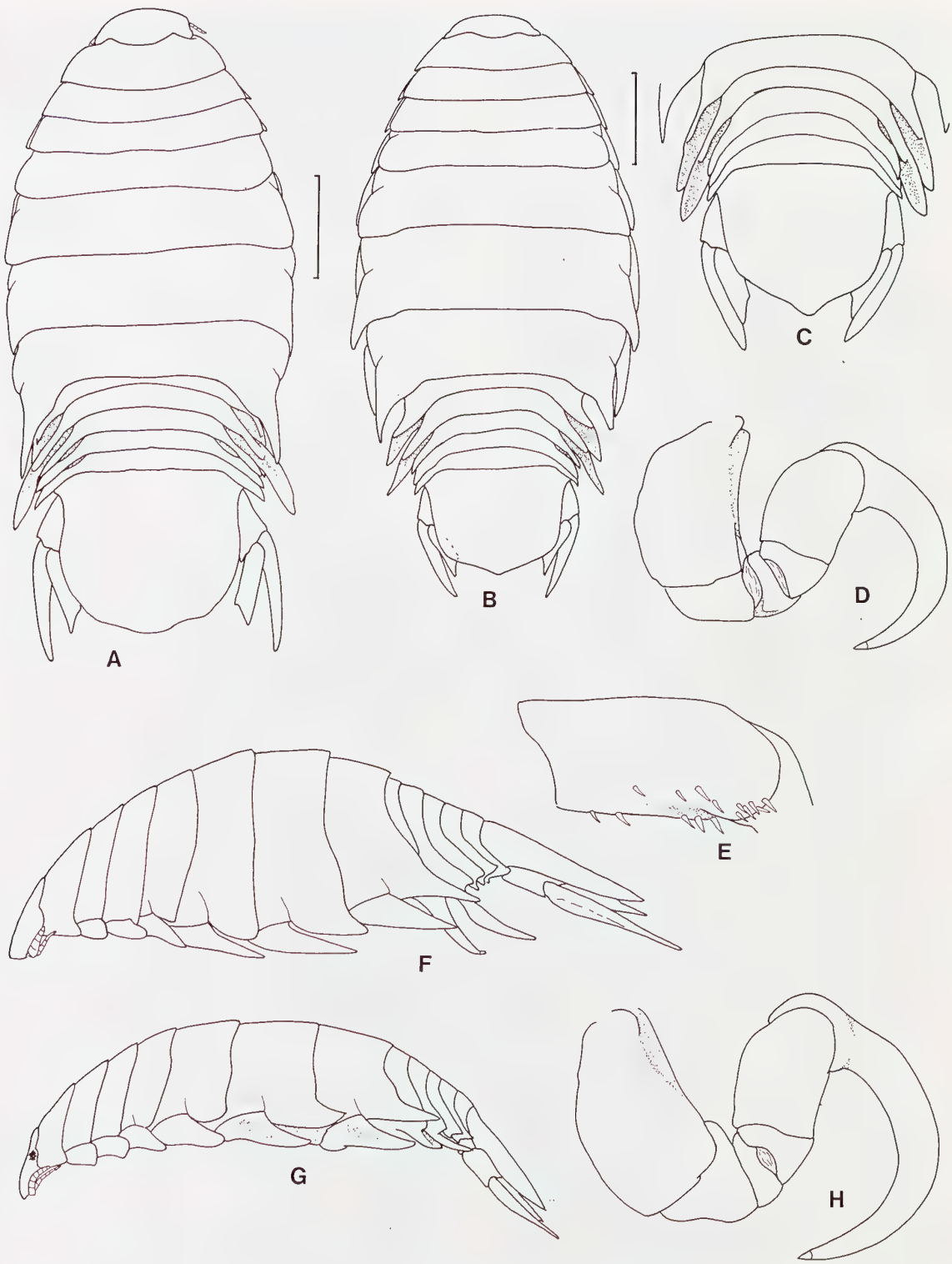

Fig. 15. *Nerocila orbignyi.* **A,** female, Palm Beach, NSW, AM P8752; **B,** female 31.0 mm, Naples, AM P37158; **C,** female 27.5 mm, Naples, AM P37158; **D,** pereopod 1, Palm Beach, AM P8752; **E,** pereopod 7, propodus, Palm Beach, AM P8752; **F,** lateral view, female, Palm Beach; **G,** female 31.0 mm, Naples; **H,** pereopod 1, female #1, Naples. Scale lines 5.0 mm.

as in female; ventrolateral margins of pleonites 1 and 2 weakly developed. Appendages similar to female except: antenna with 9 articles; mandible palp article 3 more setose; pereopods 6 and 7 more spinose; appendix masculina 0.7 length of endopod.

Colour. Specimens from Walpole, WA, black with 2 faint submedian pale longitudinal bands on pleotelson; posterior margin of pereonites and pleonites with thin clear band (this pattern corresponds exactly to that figured for North Atlantic

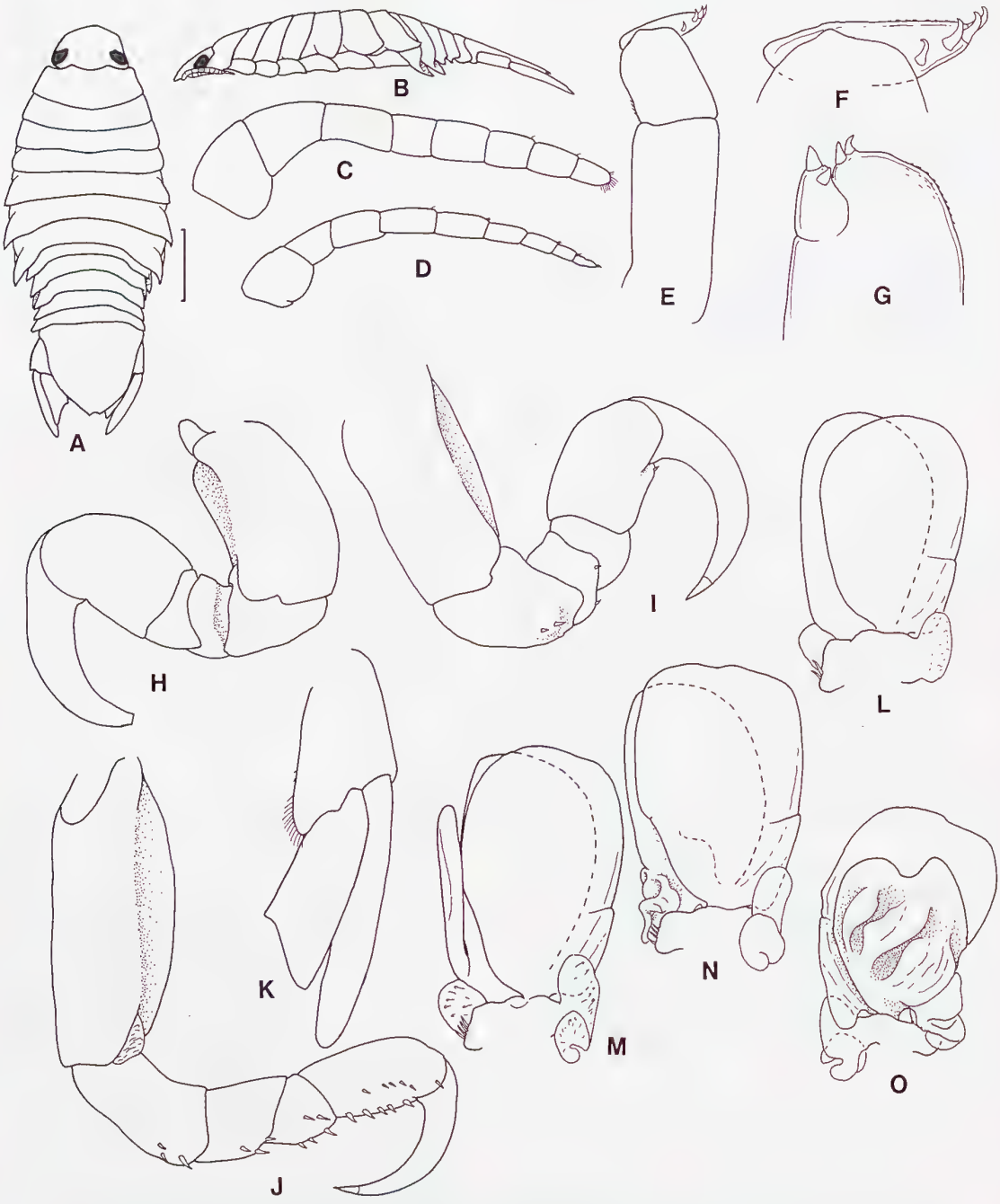

Fig. 16. *Nerocila orbignyi.* All male, Walpole, WA, AM P37149. **A,** dorsal view; **B,** lateral view; **C,** antennule; **D,** antenna; **E,** maxilliped; **F,** maxilliped article 3; **G,** maxilla apex; **H,** pereopod 1; **I,** pereopod 2; **J,** pereopod 7; **K,** uropod; **L—O,** pleopods 1—3, 5 respectively. Scale line 3.0 mm.

material by Holthuis, 1978). Most specimens pale tan, probably due to fading with age, except one female from Walpole, WA, which is pale with sparse chromatophores.

Size. Ovigerous females 18.0—34.0 mm, mean 26.2 mm (n=38); non-ovigerous females 18.0—31.0 mm, mean 22.6 mm (n=9); males 12.0—19.0 mm, mean 16.3 mm (n=6). Specimens from Tasmania and the Bass Strait were consistently larger than those from other areas, with a mean length of 32.2 mm (n=6), while the remainder (Bass Strait and Tasmania excluded) average 22.1 mm (n=32).

Variation. There is considerable variation in the degree of prolongation of the posterolateral angles of pereonites 5—7, in coxal shape, and in pleonite morphology. This variation can be found within a sample from a single host species from a single locality, and is figured for the sample from Walpole, WA, all taken from *Pseudocaranx dentex*. The posterolateral angles of the posterior pereonites may be weakly developed (Fig. 6C), strongly developed (Fig. 6B), or curved medially (Fig. 6D). The ventrolateral processes of pleonites 1 and 2 may project away from the pleon (Fig. 6D), and extend posteriorly to pleonite 4 (Fig. 6A), or beyond pleonite 5 (Fig. 6B). The posterior coxae may have concave posterior margins (Fig. 7C), convex (Fig. 7A) or straight (Fig. 7D). The uropod endopod may have a prominent distomedial point (Fig. 8F), or not (Fig. 11E); the angle of the oblique distal margin to the lateral margin may also vary. In occasional specimens, pereopod 7 has spines on the extreme distolateral surface (Fig. 9E).

In Australian material the length of pereopod 1 dactylus varies from 2.2 times longer than the propodus (Fig. 8A, Walpole, AM P37149) to 2.4 times longer than propodus (Fig. 9D, Palm Beach, AM P8752, also Bass Strait, NMV J11566). Material from Naples, Italy has pereopod 1 dactylus 2.9 times longer than the propodus (Fig. 9H, AM P37158), and this is the only apparent morphological difference between European and Australian material. Until variability in European populations can be accurately assessed, this character cannot be considered as of specific significance. The large European synonomy for this species attests to its variability.

Remarks. The history and nomenclature for this species are complex, and need full discussion. Various species have at various times been placed in synonymy with each other, frequently without recourse to illustrating or describing the material at hand. Many names involved are based on descriptions that simply cannot be restricted to a species. In the absence of type material and locality data, these names must be regarded as *nomina dubia*.

Initially I concentrated on resolving the identity and correct name for Australian and New Zealand material, which clearly involved *Nerocila macleayii* Miers, *Nerocila trailli* Filhol, *Nerocila australasiae* Schiödte & Meinert, *Nerocila novaezelandiae* Schiödte & Meinert, and *Nerocila falklandica* Cunningham. Of these, *N. trailli* and *N. novaezelandiae* were males, and although certain identification to species is not possible, they did not differ from males of Australian material. *Nerocila macleayii* Miers is a repeat of the *nomen nudum* of White & Doubleday (1843). Miers' name is predated by *Nerocila australasiae,* which also has page precedence over *Nerocila novaezelandiae.* All the species mentioned here are one species, except for those specimens of Miers from the USA and 'Africa'.

The name *Nerocila falklandica* has precedence (1871) over that of *N. australasiae* (1881), and also introduced a distributional problem. While the male type did not appear to differ from Australian material, it could not be separated from the South Atlantic species *Nerocila fluviatilis* or the species described by Dana (1853). This then linked the identified Australian material to that of South Atlantic species, and inevitably to *Nerocila orbignyi.*

The second stage lay in resolving the identity of *Nerocila orbignyi* and the species that had been placed in synonymy with it. Both Barnard (1940) and Hale (1940) separately came to the same conclusion: that material that they had at hand was *Nerocila orbignyi.* Earlier, Monod (1931) concluded much the same, but maintained that *Nerocila armata* was distinct. This finding was later supported by Brian & Dartevelle (1949). The principal species involved in this synonymy were *N. maculata, N. fluviatilis, N. cephalotes, N. rhabdota,* and *N. armata.* Most of Schiödte & Meinert's (1881) Mediterranean species had been, along with *N. affinis* Milne Edwards, synonymised with *N. maculata.* Trilles (1975a) treated all of Dana's (1853) species as valid, and also regarded *N. orbignyi* and *N. maculata* as distinct species (Trilles, 1975b). Trilles (1975a, 1975b) gave no discussion on the characters by which these species could be separated, nor how he came to make his determinations. There was no discussion on the synonyies given by Barnard (1940), Hale (1940), and Monod (1931), although these authors clearly questioned the validity of those species involved. Trilles (1975b) discussed how to distinguish *N. orbignyi* from *N. bivittata,* but not from *N. maculata. Nerocila cephalotes* had at various times been synonymised with *N. armata* or *N. rhabdota.*

Monod (1931) gave an excellent and very useful series of whole animal drawings which were of two species: *Nerocila armata* Dana and *Nerocila orbignyi* (Guérin-Méneville). Monod's figures for *N. orbignyi* correspond exactly to Australian material. Monod pointed out that the three species *N. orbignyi, N. maculata,* and *N. cephalotes* were all separated by the degree of prolongation of the posterolateral margins of pereonites 5—7. He (Monod, 1931) concluded that such variation could not be regarded as species specific and this is also clearly demonstrated by the sample from Walpole, WA (AM P37149).

Examination of the figures given by Trilles (1975b) and material in the collections of the USNM, BMNH and RMNH failed to reveal any characters by which *N. orbignyi* can be separated from *N. maculata,* and *N. maculata* is here placed in synonymy with *N. orbignyi.*

Other unresolved species involved in this wealth of names are those of Dana (1853), the Mediterranean species *Nerocila brongnartii* (Risso, 1816), *Nerocila burtiasi* Belloc, 1929, and *Nerocila cuspidata* Costa, 1851, and *Nerocila tartatowski* Popov, 1933 from the Black Sea. None of Dana's (1853) species can be confidently identified from his drawings (Dana, 1855). There are no types (most of Dana's collection was lost when the sloop *Peacock* sank off the mouth of the Columbia River, USA), and no accurate locality

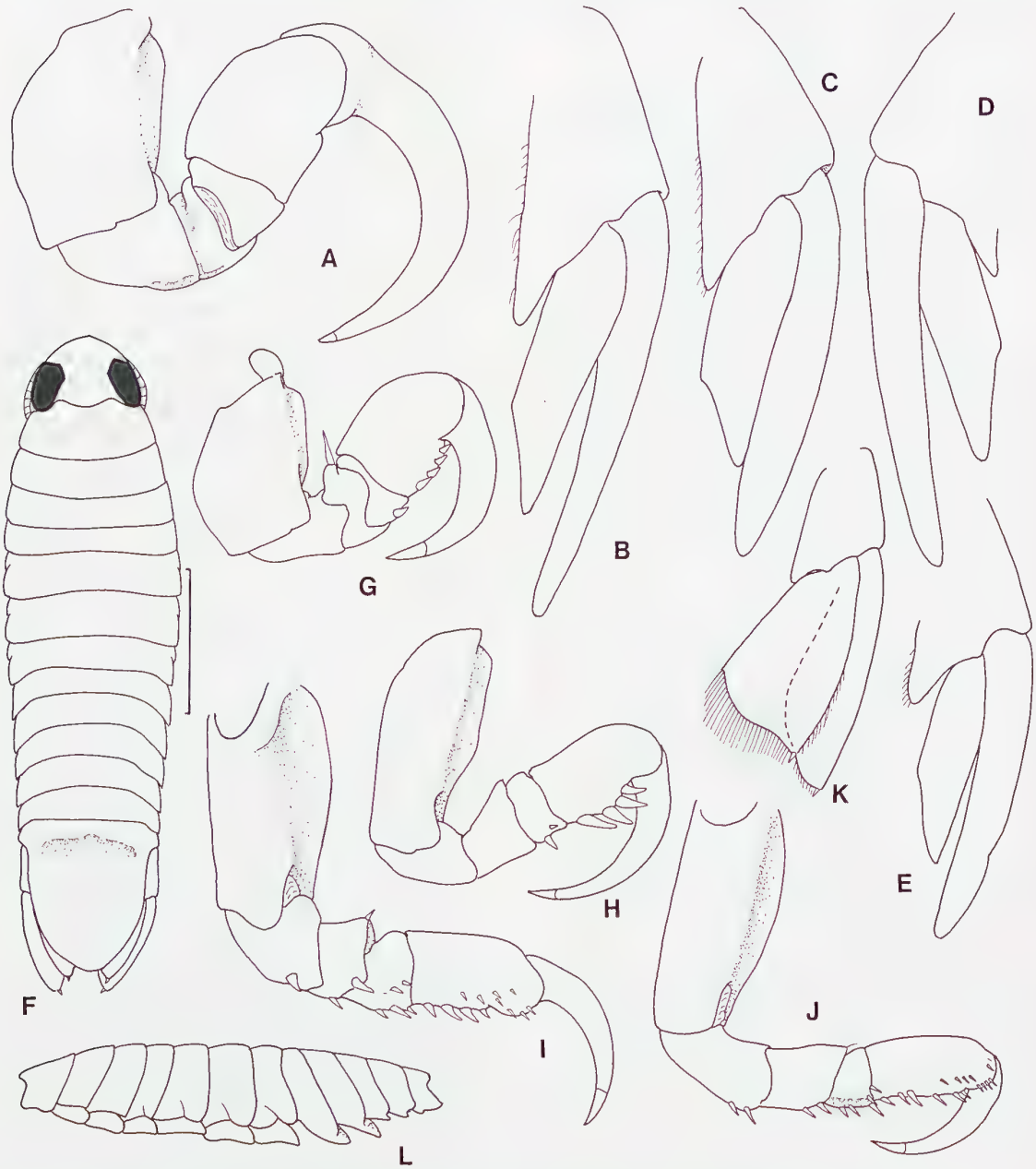

Fig. 17. *Nerocila orbignyi.* F—L, aegathoid, Walpole, WA, AM P37149; remainder as indicated. **A,** pereopod 1, female 34.0 mm, NMV J11566; **B,** uropod, female 31.0 mm, Naples; **C,** uropod, female #1, Walpole; **D,** uropod, in situ, female #2, Walpole; **E,** uropod, in situ, female #5, Walpole; **F,** dorsal view; **G—J,** pereopods 1, 3, 6, 7, respectively; **K,** uropod; **L,** lateral view. Scale line 3.0 mm.

or host data. With the exception of *N. armata,* these species are here all regarded as *nomena dubia.* Of the Mediterranean species *N. brongnartii* (transferred to *Nerocila* by Costa, 1851) and *N. cuspidata* are similarly bereft of data or types and are also relegated to *nomina dubia.* The name *Nerocila armata* Dana is conserved since it is the only one of Dana's species that has been recently characterised (Monod, 1931; Brian & Dartevelle, 1949).

The number of valid species is now reduced to three: *Nerocila armata, Nerocila fluviatilis* and *Nerocila orbignyi* (see Table 2). These species are distinguished by differences in coxa, pereonite and uropod morphology. *Nerocila armata* (Fig. 33D—K) has coxae of pereonites 2—4 and the posterolateral margins of pereonites 1—4 acute, and has longer uropods (exopod 0.9—1.1 length of pleotelson, derived from Monod, 1931, figs 1—3) with more slender rami, and an acutely pointed endopod. Australian material always has coxae 2—3 posteriorly rounded, posterolateral margins of pereonites 1—4 scarcely or not at all produced, and shorter uropods (exopod 0.6—0.9 length of pleotelson, mean 0.7). *Nerocila armata* is apparently restricted to tropical West Africa.

Nerocila fluviatilis (Fig. 35E—I) is easily distinguished from the other two species by its strongly notched uropod endopod with a distinctive sinuate lateral margin. This Atlantic species occurs along the coasts of Uruguay, Argentina, and probably Brazil, but is apparently absent from the Caribbean.

Two other species are similar to *Nerocila orbignyi: Nerocila acuminata* Schiödte & Meinert, 1881 and *Nerocila japonica* Schiödte & Meinert, 1881. *Nerocila acuminata* is easily distinguished by the uropod endopod with both margins sinuate, forming an extended acute point (Fig. 33A—C, and Brusca, 1981, figs. 11A,B, 13E). *Nerocila japonica* (Fig. 34G—J) is distinguished by the uropod endopod with straight margins which converge to an acute apex, acute lateral margins on pleonites 3—5, acute posterolateral margins of pereonites 1—4, and acute coxae of peronites 2—4.

Hosts. Trilles (1975a, 1975b) has summarised the known hosts for the totality of this species. In Australia it is recorded from *Callorhynchus milii, Acanthopagrus australis, Chrysophrys auratus, Pseudocaranx dentex* (WA specimens usually identified as "skipjack"), *Mola mola, Sillago bassensis, Pomatomus saltatrix,* and unidentified Mugilidae, Kyphosidae, and Platycephalidae. O'Connor (1978, unpublished) recorded this species from *Girella tricuspidata.* Two common names of hosts can be related to scientific names: red gurnard = *Chelidonichthye kumu;* flying gurnard = *Dactylopena orientalis.*

Distribution. Australian coasts from central New South Wales, southeastern Tasmania, Victoria, South Australia, and Western Australia to Fremantle. Widely distributed in the Mediterranean, tropical and southern Atlantic, South Africa and New

Table 2. Names involved in the synonymy of *Nerocila armata, Nerocila fluviatilis* and *Nerocila orbignyi,* and their current status (S & M = Schiödte & Meinert, 1881; all nomina nuda are also synonyms of *N. orbignyi*).

NAME	STATUS	SOURCE
N. orbignyi (Guerin-Meneville)	valid	priority
N. maculata Edwards	*N. orbignyi*	specimens
N. affinis Edwards	*N. orbignyi*	literature
N. Mac Leaii White & Doubleday	nomen nudum	this work
N. vittata Lucas	*N. orbignyi*	literature
N. brongnartii (Risso)	nomen dubium	literature
N. cuspidata Costa	nomen dubium	literature
N. aculeata Edwards	nomen dumium	literature
N. aculeata Dana	nomen dubium	literature
N. armata Dana	valid	specimens
N. brasiliensis Dana	nomen dubium	literature
N. latiuscula Dana	nomen dubium	literature
N. tenuipes Dana	nomen dubium	literature
Livoneca scianae Beneden	nomen nudum	Holthuis, 1978
N. falklandica Cunningham	nomen dubium	holotype
N. rhabdota Koelbel	*N. armata*	literature
N. adriatica S & M	*N. orbignyi*	literature
N. australasiae S & M	*N. orbignyi*	holotype
N. cephalotes S & M	*N. orbignyi*	specimens
N. fluviatilis S & M	valid	specimens
N. neapolitana S & M	*N. orbignyi*	literature
N. novaezelandiae S & M	*N. orbignyi*	types
N. macleayii Miers, et auct.	*N. orbignyi*	types
N. trailli Filhol	*N. orbignyi*	holotype
N. laticeps Bovallius	*N. orbignyi*	literature
Rosca rogans Stebbing	*N. orbignyi*	types
N. burtiasi Belloc	uncertain	literature
N. tartatowski Popov	*N. orbigny*	literature

Zealand. Apparently absent from the tropical Indo-Pacific (except for one specimen from Eilat), North Pacific, East Pacific and western North Atlantic.

Nerocila phaiopleura Bleeker
Figs 18, 19

Nerocila phaiopleura Bleeker, 1857: 25, pl. 1, fig. 3.—Monod, 1976: 857; Trilles, 1979: 253, pl. 1, fig. 3.
Nerocila phaeopleura.—Miers, 1880: 467; Schiödte & Meinert, 1881: 13, pl. 1, figs 6, 7; Gerstaecker, 1882: 260; Nierstrasz, 1915: 75, pl. 3, figs 1, 2; 1918: 113, pl. 9, figs 6, 7; 1931: 124; Barnard, 1925: 392; 1936: 164, figs 6a—c; Chilton, 1926: 180, figs 3a—b; Monod, 1934: 12; Serène, 1937: 69; Morton, 1974: 143, pl. 1; Kensley, 1978: 82:, fig 33D,G.
Nerocila (Nerocila) phaeopleura.—Bruce, 1982: 316, fig 1, 4a—c.
Nerocila (Nerocila) phaiopleura.—Bowman & Tareen, 1983: 5, fig. 5.
Nerocila sp. Monod, 1976: 857, figs 14, 15.

Material examined. Two females (ovig 13.7, 14.0), Batavia, Java, Indonesia, on *Stolephorus indicus,* one still attached anterior to caudal peduncle of host (RMNH 1322). Female (ovig 15.5), Java Zee, Indonesia, coll. P. Buitendijk (RMNH 11). Female (non-ovig 21.0), Conway Beach, near Proserpine, Qld, Nov 1971, on caudal peduncle of *Liza argentea,* coll. R. Harrison (QM W4824). Female (ovig 13.5), aegathoid (12.5), Swan River, WA, 1984, on *Cnidoglannus macrocephalus,* coll. A. Williams (AM P37160). 2 females (ovig 13.5, 15.0), middle estuary, Swan River, WA, Dec 1984, on *Engraulis australis,* coll. A. Williams (AM P37161). Female (non-ovig 11.5), Swan River, WA, ca. 1986, on base of ventral fin of *Engraulis australis,* coll. A. Williams (WAM 2330—86).

Types. The types are held at the Rijksmuseum van Natuurlijke Historie, Leiden.

Type locality. Batavia Bay (= Jakarta), Indonesia (Bleeker, 1857).

Descriptive notes. Eyes large, about 0.5 width of cephalon. Pleonites 1 and 2 with ventrolateral margins weakly produced. Mandible palp article 1.5 times longer than article 2. Lateral margin with about 22 stout setae. Maxilliped article 3 with 4 recurved spines. Pereopods 1—5 with weak swelling on anteroproximal margin of dactylus; pereopod 7 with 2 spines on posterior margin of propodus. Uropod slender, tapering exopod, 1.7—2.1 times longer than endopod; endopod apex narrowly rounded or obliquely truncate.

Male. Not known.

Aegathoid. The specimen figured in Fig. 19 is at the "aegathoid" stage.

Variation. The female from Proserpine is an intermoult which exaggerates the apparent width. This specimen differs from others in having the uropod endopod with an obliquely truncate apex. However the other appendages all correspond exactly to those of specimens from Hong Kong (Bruce, 1982) and Kuwait (Bowman & Tareen, 1983). Swan River specimens, when compared to other material, all have a narrower body shape, shorter cephalon, cephalon anterior margin bent ventrally and posteriorly, short posteriorly round coxae, pereonite posterolateral angles not extended, and large eyes with distinct ocelli.

Remarks. *Nerocila phaiopleura* is a widely distributed and variable species. It can be recognised by the large eyes (or traces of), lack of posterolateral processes on the pereonites, pleotelson curving smoothly to a distinct point, narrow and straight uropod rami, and the distinctive pereopod morphology.

Hosts. In Australia: *Liza argentea, Cnidoglannus macrocephalus* and *Engraulis australis.* Previous records are given by Bowman & Tareen (1983), and hosts are all from the families Engraulidae and Clupeidae. Barnard's (1936) record from *Xiphias gladius* (swordfish) is surely in error, the isopod probably having come from swordfish prey.

Distribution. Proserpine, Queensland, and the Swan River estuary, Western Australia; also widely recorded from South Africa and Kuwait to Hong Kong (Bowman & Tareen, 1983).

Emphylia group species

Nerocila monodi Hale
Figs 20—22

Nerocila serra.—Hale, 1926: 208, fig. 6.
Nerocila monodi Hale, 1940: 301, fig. 8.—Bowman & Tareen, 1983: 7; Roubal, Armitage & Rhode, 1983: 3.

Material examined. HOLOTYPE, female (ovig 17.7), Great Palm Island, Queensland, no date, on *Lutjanus,* coll. Dr. W.E.J. Paradice on HMAS *Geranium* (SAM C290). NON-TYPE. Female (ovig 22.5), Arafura Sea, N.T., 10°02.55'S, 136°46.45'E, 7 Feb 1986, depth 53 m, on *Carangoides humerosus,* coll. J.B. (NTM Cr3623). Female (ovig 22.0), north of Smith Point, NT, 11°07'S, 132°08'E, 18 Oct 1981, depth 27 m, coll. H.K. Larsen (NTM Cr737). Female (ovig 18.0), Fake Creek, Shoal Bay, Darwin, NT, 4 Apr, 1975, coll. N.T. Div. Fish (NTM Cr771). Female (non-ovig 21.0), Talle Breakwater, northern Qld, 25 Feb 1983, on "red bream", coll. D. Baldwin (AM P37157). Female (ovig 22.0), Tin Can Bay, southeastern Qld, 10 Dec 1973, from *Rhabdosargus sarba,* coll. R. Harrison (QM W4827). 4 females (ovig 27.0, non-ovig 19.5, 22.0, ca 26.0), Weiba Creek, Noosa, southeastern Qld, 16 Mar 1975, on *Acanthopagrus australis,* coll. R. Harrison (QM W4825). 2 females (ovig 21.5, non-ovig 19.5), Moreton Bay, Qld, 13 May 1982, one on each side of tail of *Priacanthus macracanthus,* coll. S.M. Wilson (QM W11007). 2 females (ovig 21.5, 22.5), Brisbane River, Qld, 5 May 1952, one on each side of tail of "perch", don. A.C. Gardiner (QM 9485). Female (non-ovig 26.0), male (14.0), Victoria Point, Moreton Bay, Qld, 31 Mar 1975, on *Acanthopagrus australis,* coll. R. Monroe (QM W4826). Female (ovig 21.5), 2 males (14.0, 15.0), Jacobs Well, Southport, Qld, 22 May 1975, on tail of "bream", coll. H. Linton (QM 4814).

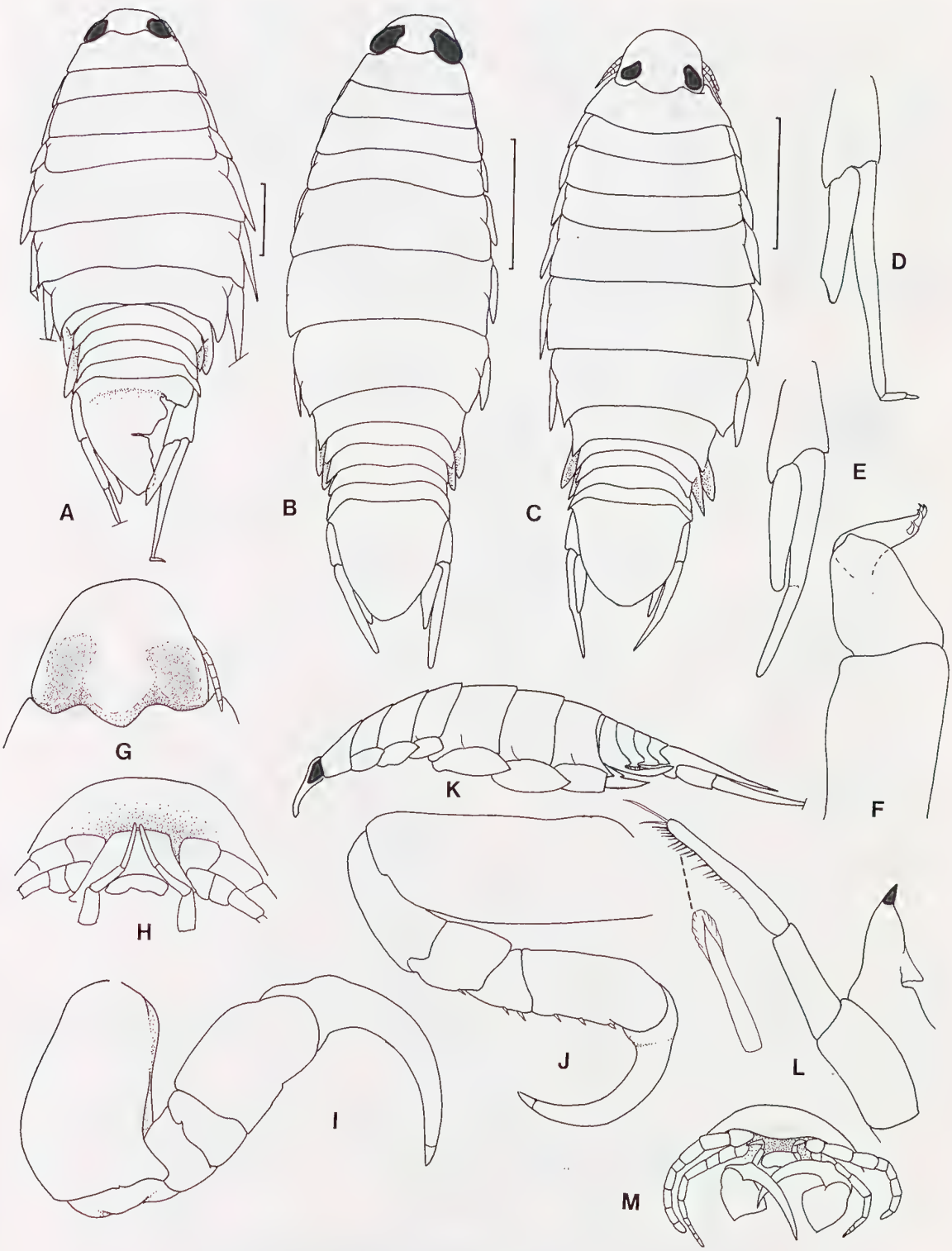

Fig. 18. *Nerocila phaiopleura.* Female, Qld, QM W4824, except where indicated. **A,** dorsal view; **B,** female 15.0 mm, Swan River; **C,** female 14.0 mm, RMNH 1322; **D,** uropod; **E,** uropod, RMNH 1322; **F,** maxilliped; **G,** cephalon; **H,** frons; **I,** pereopod 1; **J,** pereopod 7; **K,** lateral view; **L,** mandible palp; **M,** buccal area, female, Swan River. Scale lines 3.0 mm.

Additional material. Female, North West Shelf, WA, 19°27.1′S, 118°58.4′E, 8 Dec 1982, 36m, coll. C.C. Lu (NMV J11572). Female, Arafura Sea, 12°58.0′S, 132°10.0′E (NTM Cr736). Female, Arafura Sea, 10°56′S, 133°34′E, 18 Sep 1986, ca. 50 m, on *Nemipterus hexadon,* coll. fisheries observer on Thai trawler (NTM Cr4560). Female, Arafura Sea, 10°15′S, 136°40′E, 20 Feb 1986, 55—60 m, fisheries observer on Taiwanese trawler (NTM Cr4559). Female, Cleveland Bay, Townsville, Qld, 4 Dec 1986 on *Pomadasys hasta* coll. B. Ingram, (AM P37156). 2 females, Running Creek, Fraser Island, Qld, 2 July 1975 on "bream", coll. P. Shanco (QM W5741). Female, Noosa River, above Lake Cooroibah, on bream (QM W8763). Female, Bribie Island, Moreton Bay, Qld, on *Acanthopagrus australis* (QM W10266). Female, Burpengary Creek, Moreton Bay, Qld, 1899, coll. Dr. Bancroft (QM W5750). Female, Redcliffe, Moreton Bay, Qld, on "snapper", don. R.L. Cribb (QM G13/241). Female, Redcliffe, Moreton Bay, Qld, don. L.D. McIntosh (QM W9484). Female, St. Helena Island, Moreton Bay, Qld. 19 May 1982, coll. A. Bradshaw (QM W10267). 2 females, Wellington Point, Moreton Bay, Qld, 28 Mar 1974, on "black bream", coll. H. Sommerfeldt (QM W4875). Female, male, Victoria Point, Moreton Bay, on *Acanthopagrus australis* (QM W4826). Female, Brisbane River, Qld, 9 Jan 1893, don. J.P. Bichard (QM W5751). Female, Brisbane River, Qld, on tail of "perch" (QM W9486). Female, Brisbane River, Qld, on tail of "bream", coll. Mrs. M. Kubo, (AM P37162). Female, Moreton Bay, on bream (QM W5762). Female, Southport, southeastern

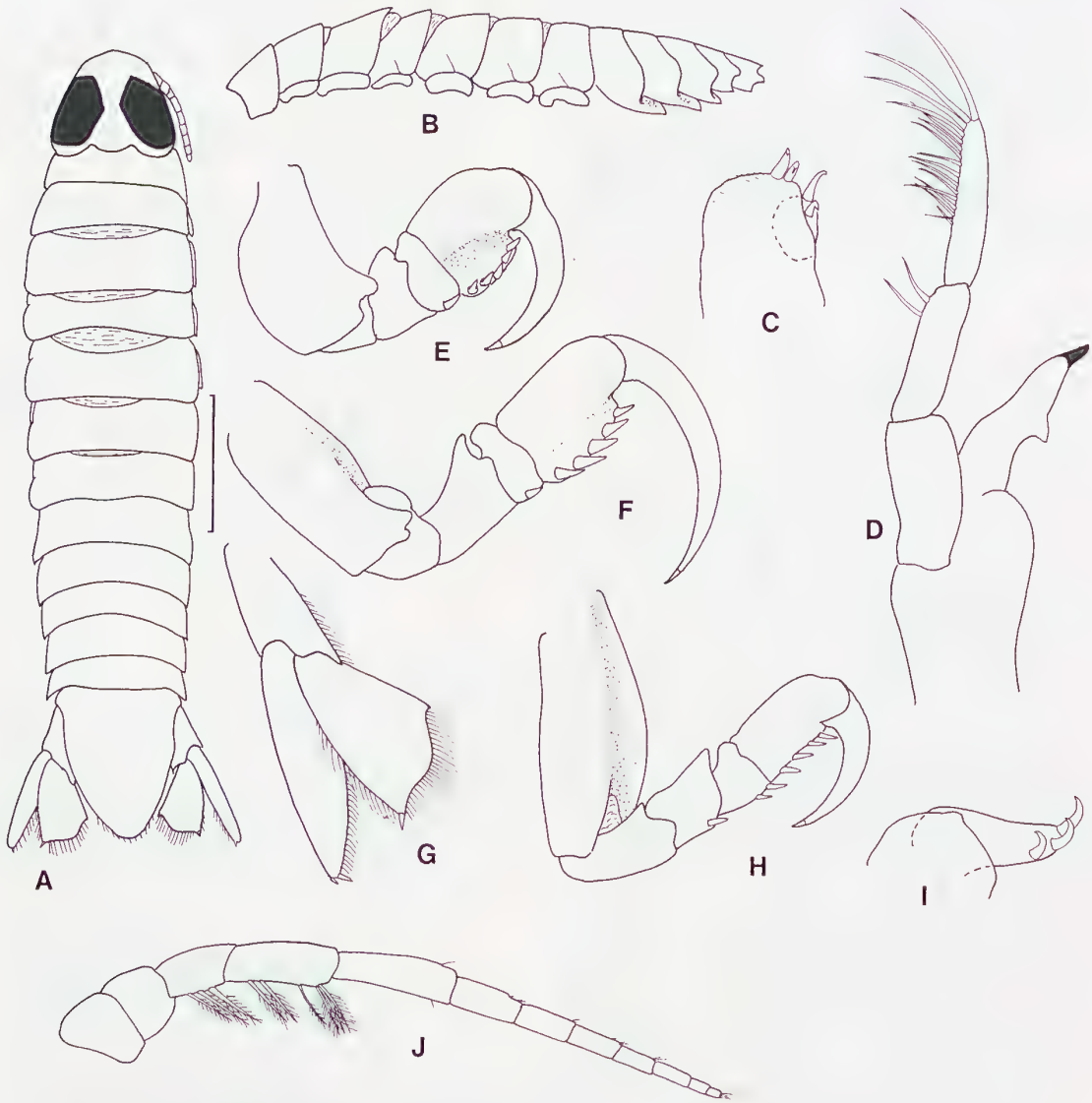

Fig. 19. *Nerocila phaiopleura.* All aegathoid, Swan River, WA, AM P37160. **A,** dorsal view; **B,** lateral view, pereon, pleon; **C,** maxilla apex; **D,** mandible; **E,** pereopod 1; **F,** pereopod 3; **G,** uropod; **H,** pereopod 7; **I,** maxilliped apex; **J,** antenna. Scale line 2.0 mm.

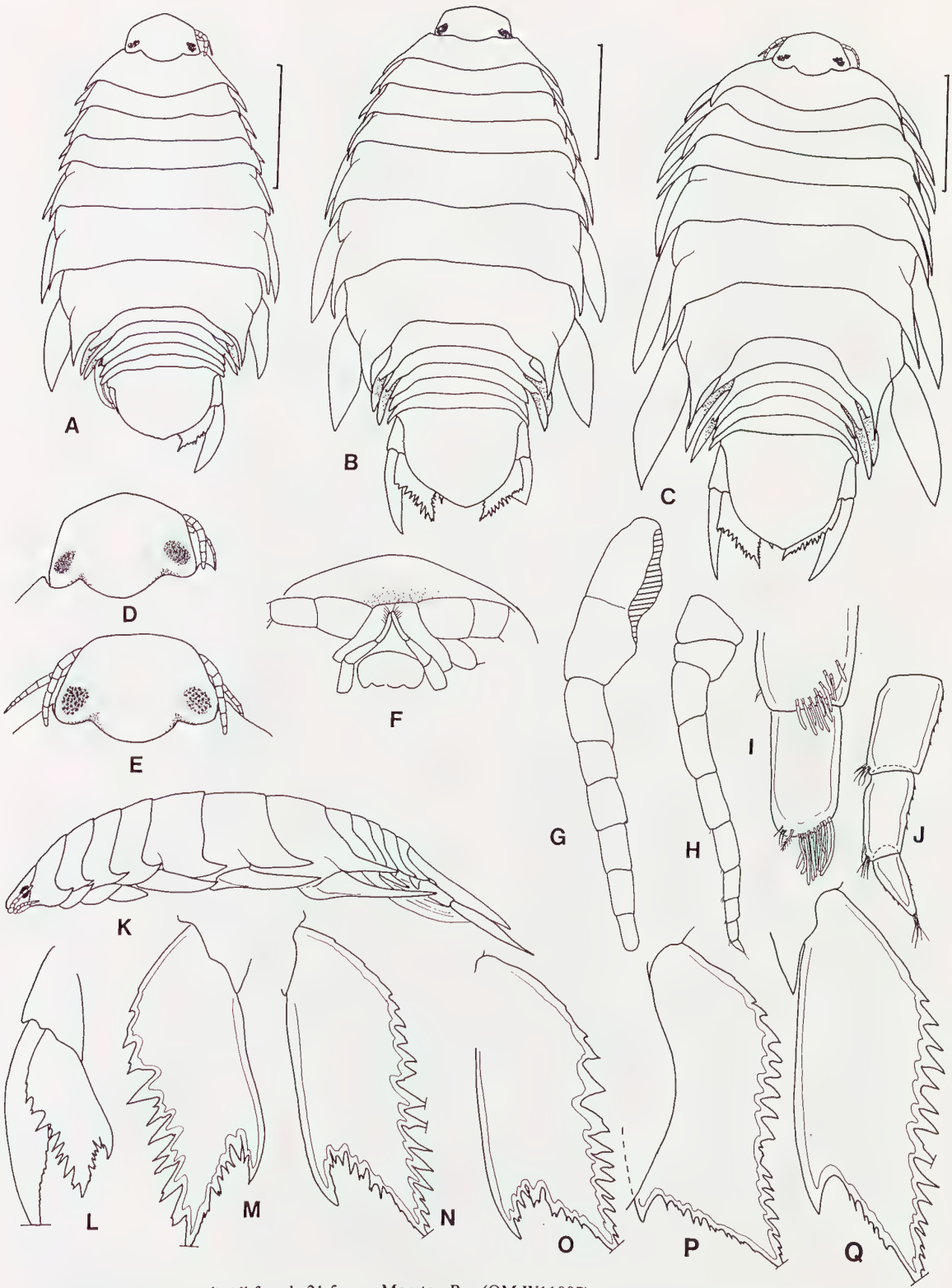

Fig. 20. *Nerocila monodi.* All female 21.5 mm, Moreton Bay (QM W11007), except where indicated. **A,** holotype; **B,** dorsal view; **C,** female, NT (NTM Cr737); **D,** cephalon, holotype; **E,** cephalon; **F,** frons, holotype; **G,** antennule; **H,** antenna; **I,** antennule, distal articles; **J,** antenna, distal articles; **K,** lateral view; **L,** left uropod; **M,** left uropod, endopod; **N,** right uropod, endopod; **O,** right uropod endopod, female non-ovig QM W11007; **P,** right uropod endopod, female 27.0 mm, QM W4825; **Q,** right uropod endopod, female 22.0 mm, QM W4825. Scale lines 5.0 mm.

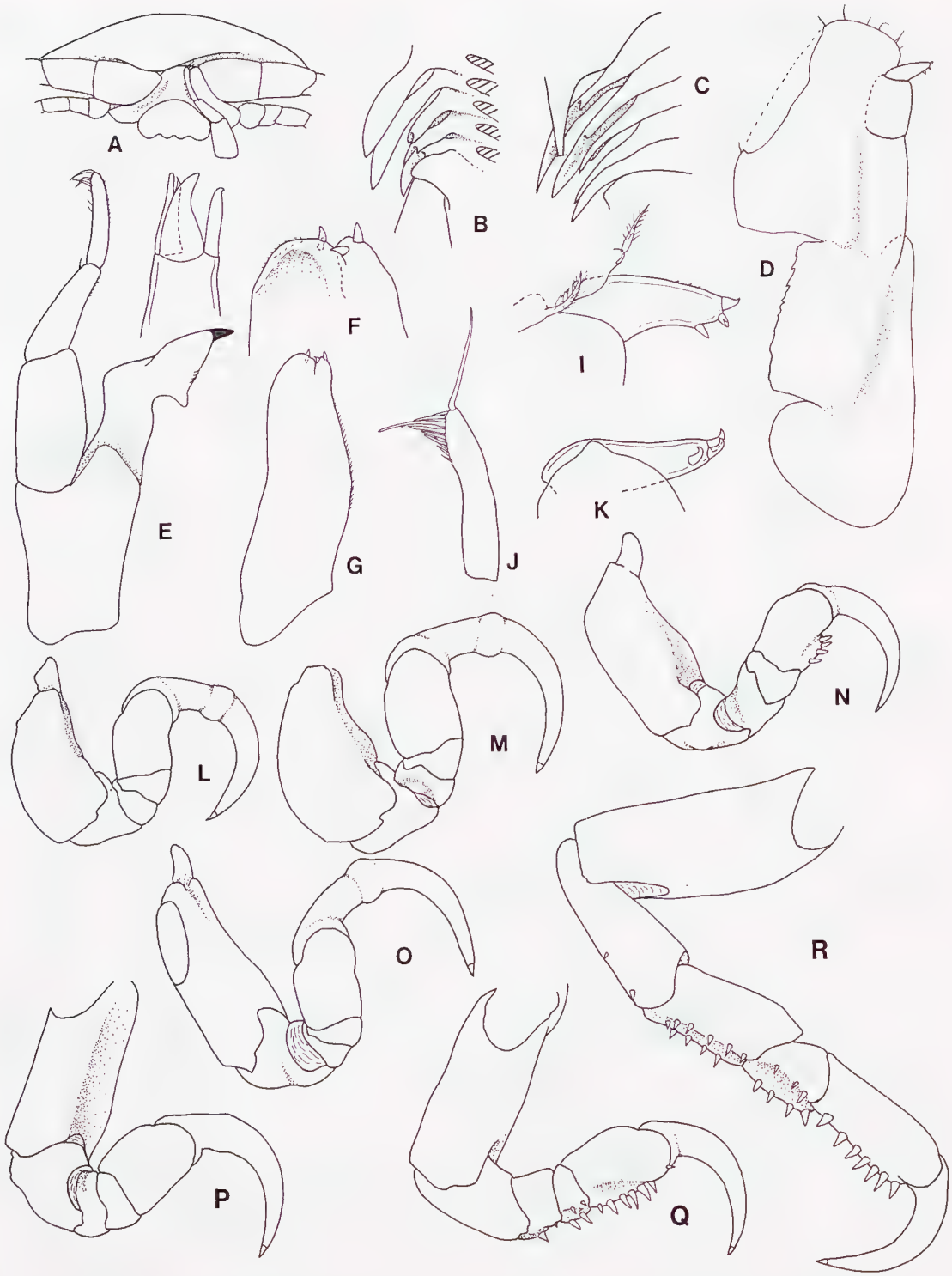

Fig. 21. *Nerocila monodi.* Figs of female ovig, Moreton Bay (QM W11007), except where indicated. **A,** frons, non-ovig female, QM W11007; **B,** ventral view, right pleonites, non-ovig female, QM W11007; **C,** left pleonites, female, NTM Cr3623; **D,** maxilliped; **E,** mandible; **F,** maxilla apex; **G,** maxilla; **H,** maxillule apex; **I,** maxilliped article 3; **J,** mandible palp article 3; **K,** maxilliped article 3, non-ovig female, QM W11007; **L—R,** pereopods 1—7 respectively.

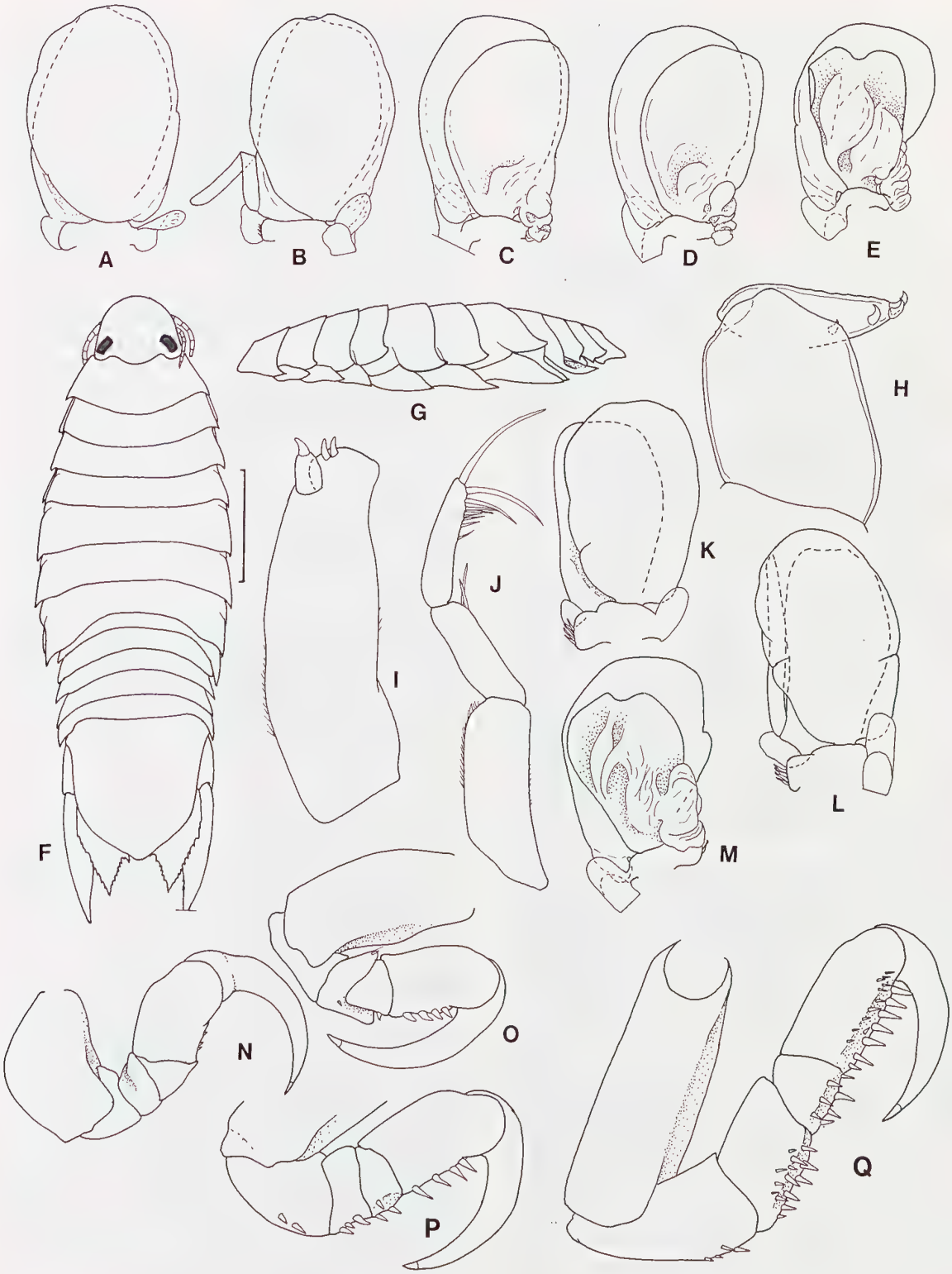

Fig. 22. *Nerocila monodi.* **A—E,** pleopods 1—5 respectively (3—5 in posterior view); remainder male 15.0 mm, Jacob's Well (QM W4814); **F,** dorsal view; **G,** lateral view, pereon, pleon; **H,** maxilliped apex; **I,** maxilla; **J,** mandible palp; **K—M,** pleopods 1, 2, 5; **N—Q,** pereopods 1, 3, 6, 7 respectively. Scale line represents 3.0 mm.

Qld, from "squire", coll. E. Pohlman (QM 9482). 2 females, Tuggerah Lakes, NSW, Mar 1957, on tail of bream, coll. A.A. Racek (AM P13147).

Types. Hale (1940) only designated a holotype but there is another specimen labelled paratype (SAM C289). The whereabouts of other material he examined is uncertain.

Type locality. Great Palm Island, Queensland.

Description of female. Body about 2.0 times as long as wide. Cephalon anterior margin subtruncate, eyes small, about 0.3 width of cephalon. Posterolateral margins of all pereonites produced, acute, not bent dorsally. Coxae all posteriorly acute, those of pereonites 2—4 not longer than segment, those of 6 and 7 longer than segment. Pleonite 1 longest; ventrolateral margins of pleonites 1 and 2 produced as far as pleonite 5, curving posteriorly; pleonites 3—5 lateral margins acute. Pleotelson 0.8 as long as wide, lateral margins convex, converging to indistinct apical point.

Antennule extending to pereonite 1, articles 1 and 2 appearing fused, much wider than article 3; antenna with 10 articles.

Mandible palp article 1 longest; article 3 with about 7 setae on distolateral margin. Maxilliped article 3 with 3 slender hooked spines.

Pereopods 1, 2, 4 and 5, without spines, dactylus with swelling about 0.3 along its length; pereopods 3, 5 and 7 dactylus without swelling, with spines. Pereopods 1 and 2 dactylus about 2.6 times longer than propodus. Pereopod 7 dactylus about 1.2 times longer than propodus. Pereopod 3 with propodal palm weakly lobate, with 4 spines. Pereopod 6 with 2 spines on posterior margin of merus, carpus with 4 spines in 2 rows, and propodal palm with 6 spines. Pereopod 7 with 2 spines on posterior margin of ischium, merus with 2 rows of 6 and 4 spines, merus with 2 rows of 3 and 4 spines, propodus with 7 large conical spines.

Pleopod 2 appendix masculina about 0.7 length of endopod. Pleopods 3 and 4 endopod with single weak lobe. Pleopod 5 with 2 large folds. Uropod exopod lanceolate, apex acute, about 1.4 times longer than endopod; medial margin finely serrate. Endopod lateral margin strongly serrate; distal margin excavate and serrate, with distomedial point; lateral margin straight.

Male. About 3 times as long as wide. Cephalon anterior margin rounded. Coxae and postolateral angles of pereonites less strongly produced than in females. Appendages similar to those of female but for: mandible palp articles 2 and 3 with more and larger setae; maxilliped article 3 with 4 large spines; pereopods without nodules, and all with spines; pleopod 2 appendix masculina as long as endopod. Uropod endopod with serration less developed.

Colour. Deep red to pale tan, often with 3 distinct longitudinal bands.

Size. Ovigerous females 18.0—28.0 mm (mean 22.8, n=20); non-ovigerous females 16.0—25.0 mm (mean 19.8, n=8); males 14.0—15.5 mm (mean 14.8 mm, n=3).

Variation. Most of the variation shown by this species is covered by the illustrations given here. Serration of the uropods is never identical, not even between the left and right uropods of a single specimen. The length of the coxae and posterolateral pereonite extensions also varies, but not greatly. A notable variation is that specimens from the Northern Territory consistently had the anterior pereonites (1 to 4) wider than in material from eastern Australia.

Remarks. This species is easily recognised, being the only Australian species with both margins of the uropod endopod serrate. Bowman & Tareen (1983) gave a key to all species of *Nerocila* with serrate endopods, and *N. monodi* is easily distinguished by being the only one with a serrate distal margin.

Hosts. Recorded from a variety of fish families, but occurs most commonly on Sparidae: *Acanthopagrus australis, Rhabdosargus serba,* and *Chrysophrys auratus* (recorded as "snapper" or "squire"). Also recorded from *Carangoides humerosus, Nemipterus hexadon, Priacanthus macracanthus, Pomadasys hasta* and, by Hale (1940), *Lutjanus* sp.

Distribution. Recorded commonly along the Queensland coast from Southport to Cairns (Hale, 1940); also Northern Territory, North West Shelf; two records from New South Wales: Port Stephens (Roubal et al., 1983) and Tuggerah Lakes.

Nerocila serra Schiödte & Meinert

Nerocila Serra Schiödte & Meinert, 1881: 17, pl. 1, figs 12—14.

Nerocila serra.—Gerstaecker, 1882: 260; Stebbing, 1893: 352; Nobili, 1903: 39; Nierstrasz, 1915: 74; 1931: 124; Barnard, 1925: 392; 1936: 163; Pillai, 1954: 12; Kensley, 1978: 81, fig. 33E; Bowman, 1978: 35; Bowman & Tareen, 1983: 12, fig. 13.

Nerocila trivittata.—Trilles, 1979: 254, pl. 1, fig. 4.

Material examined. Female, collected pre-1891, unlocalised northwestern Australia (BMNH unreg.).

Remarks. The specimen examined was in a jar containing three other cymothoids: *Creniola saurida* (data: — N.W. Australia); *Ceratothoa* sp. (data: — Roebuck Bay, WA, BMNH 91.6 20.25); *Lironeca raynaudii* (data: — Van Deimen's Land). It is therefore not unreasonable that the specimen of *N. serra* did come from Western Australia.

The species is not redescribed as there is no material in good condition from Australia. The reader is referred to Bowman & Tareen (1983) for figures and comments.

Creniola n. gen.

Diagnosis of female. Body 2.0—2.5 times as long

as wide, dorsally vaulted. Cephalon anterior margin wide, not rostrate, not folded under; posterior margin distinctly trilobed. Pleonites all subequal in width, pleon usually as wide as pereon, occasionally slightly (0.65) narrower; ventrolateral margins of pleonites 1 and 2 not produced; ventrolateral margin of all pleonites with small process. Mandible palp slender, elongate, article 1 longest, article 3 with setae on distolateral margin. Pleopods as for *Nerocila.*

Additional characters. Body widest between pereonites 4—6. Coxae not extending beyond posterior of pereonites, scarcely or not visible in dorsal view. Pleotelson short. Antennule 8 articled; antenna with up to 11 articles. Maxillule with 4 terminal spines. Maxilla with medial lobe partly fused to lateral, 2 spines on each lobe. Maxilliped article 3 with 3 recurved spines. Pereopods 1—6 gradually increasing in length; pereopod 7 subequal in length to pereopod 6. Brood pouch made of 5 pairs of oostegites arising from coxae 1, 2, 3, 4, and 6, and posterior pocket; last pair of oostegites extending posteriorly over pleopods. Pleopods as for *Nerocila* but endopod of pleopods 1 and 2 smaller than exopod; pleopod 1 exopod much larger than 2, rami of pleopods 2—5 decreasing in size. Uropods short, not extending posterior to pleotelson.

Type species. *Nerocila laticauda* Schiödte & Meinert, 1881, by original designation. Holotype held at the MNHN, Is. 623.

Composition. *Crenolia saurida* (Avdeev, 1977) **n. comb**, *Crenolia breviceps* (Schiödte & Meinert, 1881), **n. comb**, *Crenolia laticauda* (Schiödte & Meinert), **n. comb.**

Etymology. The name continues Leach's tradition of using anagrams based on Caroline. Gender is feminine.

Remarks. The genus is immediately distinguished from *Nerocila* by the wide pleon, and lack of extended ventrolateral processes on pleonites 1 and 2. Other differences are: pleopod 1 much larger than 2 (subequal in *Nerocila);* coxae concealed in dorsal view (visible in *Nerocila);* uropods not extending beyond pleotelson (always extend beyond pleotelson in *Nerocila).*

It should be emphasised that the difference in pleonal morphology between *Creniola* and *Nerocila* is substantial. Comparison of morphologies of related genera such as *Anilocra* (see Bruce, 1987a, Williams & Williams, 1981), and *Renocila* (see Bruce, 1987b, Williams & Williams, 1980), show that pleon morphology is constant within a genus. *Anilocra, Pleopodias* and *Renocila* all have substantial differences in mandible palp morphology as well. Lack of mouthpart differences between *Nerocila* and *Creniola* merely indicate that these two genera are closely allied, as are *Pleopodias* and *Anilocra.*

Key to Australian Species of *Creniola*

1. Posterolateral margins of pereonites 5—7 not produced; pereopods without processes. ..... *C. saurida*

——Posterolateral margins of pereonites 5—7 produced; pereopods 6 and 7 ischium posterodistal margin produced. ..... *C. laticauda*

Creniola laticauda (Schiödte & Meinert)
Figs 23—25

Nerocila Blainvillei.—Schiödte & Meinert, 1881: 78, pl. VI, figs 11, 12 (not *N. blainvillii* Leach, 1818).

Nerocila Blainvillii.—Schiödte & Meinert, 1881, figs 11, 12 (lapsus).

Nerocila laticauda Schiödte & Meinert, 1881: 81, pl. VI, figs 14, 15.—Gerstaecker, 1882: 262; Whitelegge, 1902: 235; Hale, 1926: 203, figs 1g, 2, 3; 1929: 259, figs 254, 257, 258; 1940: 300; Nierstrasz, 1931: 125; Trilles, 1975a: 319, pl. II, fig. 14; Moreira & Sadowsky, 1978:100, 113, 122, 134; Beumer et al., 1982: 32; Hooper, 1983: 42.

Material examined. HOLOTYPE: female (non-ovig 20.5), Neue Hollande, Quoy et Gaimard, 11-2-1829 (MNHN Is. 263). NON-TYPE: Female (non-ovig 19.0), La Perouse, NSW, ca. 1898, don. J.D. Ogilvy (AM G1799). Female (non-ovig 23.0), Jervis Bay, NSW, 22—23 May 1973, trawled, coll. NSW SF (AM P19583). Female (ovig 21.0), Portsea, Vic., 10 Feb 1976, parasite on fish (NMV J11571). Female (ovig 26.0), male (11.0), Port Willunga, SA, no other data, coll. S. Howe (SAM C286). Female (non-ovig 34.0), 8.7 km off Venus Bay, SA, 11 Apr 1982, in prawn trawl, coll. K. Paul, D. Craig on *Cavalier* (SAM TC4481). Female (ovig 36.0), 110 km southeast of Eyre, WA, 33°04′S, 127°12′E, 1 Aug 1981, depth 91 m, coll. CSIRO *Soela* (SAM TC4483).

Additional material. New South Wales: female, between Newcastle and Port Stephens, Sept 1926, 146 m, coll. trawler *Gunner* (AM P8752). Female, 11 km east of Cape Three Points, 33°32′S, 151°35′E, 25 Feb 1898, sticky mud and shell, 82 m. coll. HMCS *Thetis* (AM G2203). Female, Port Jackson, Dec 1908 (AM P5621). Male, east of Port Hacking, 34°05′S, 151°15′E, 11 Mar 1898, mud, 92 m, coll. HMCS *Thetis* (AM G2401). Female, 6 km east of Jibbon, 34°16′S, 151°04°E, 18 Mar 1898, sand, mud, rock, 100 m, coll. HMCS *Thetis* (AM P1563). Female, 11 km east of Kiama, Mar 1927, on John Dory, *Zeus* sp. 73—91 m, coll. trawler *Bar-ea-mul* (AM P8819). 2 females, 16 km northwest of Montague Island, 5 Sept 1926, 55—73 m, coll. W. Boardman on trawler *Gunner* (AM P10681). 3 females, 29 km south of Montague Island, Mar 1927, 91—110 m, on *Platycephalus* sp., coll. trawler *Bar-ea-mul* (AM P8817). Female, north of Montague Island, Apr 1927, from *Platycephalus* sp., coll. trawler *Bar-ea-mul* (AM P8826). 3 females, east of Wattamolla, 34°12.5′S, 151°13′E, 13 Mar 1898, 133 m, coarse sand, shell, coll. HMCS *Thetis* (AM P3329). Victoria: Female, Port Phillip, Aug 1922, coll. J.B. Wilson (AM P5823). Female, Portsea, Port Phillip Bay, 10 Feb 1976, parasite on fish (NMV J11571). South Australia: Female (+ 2 broken specimens), Kingston, no other data

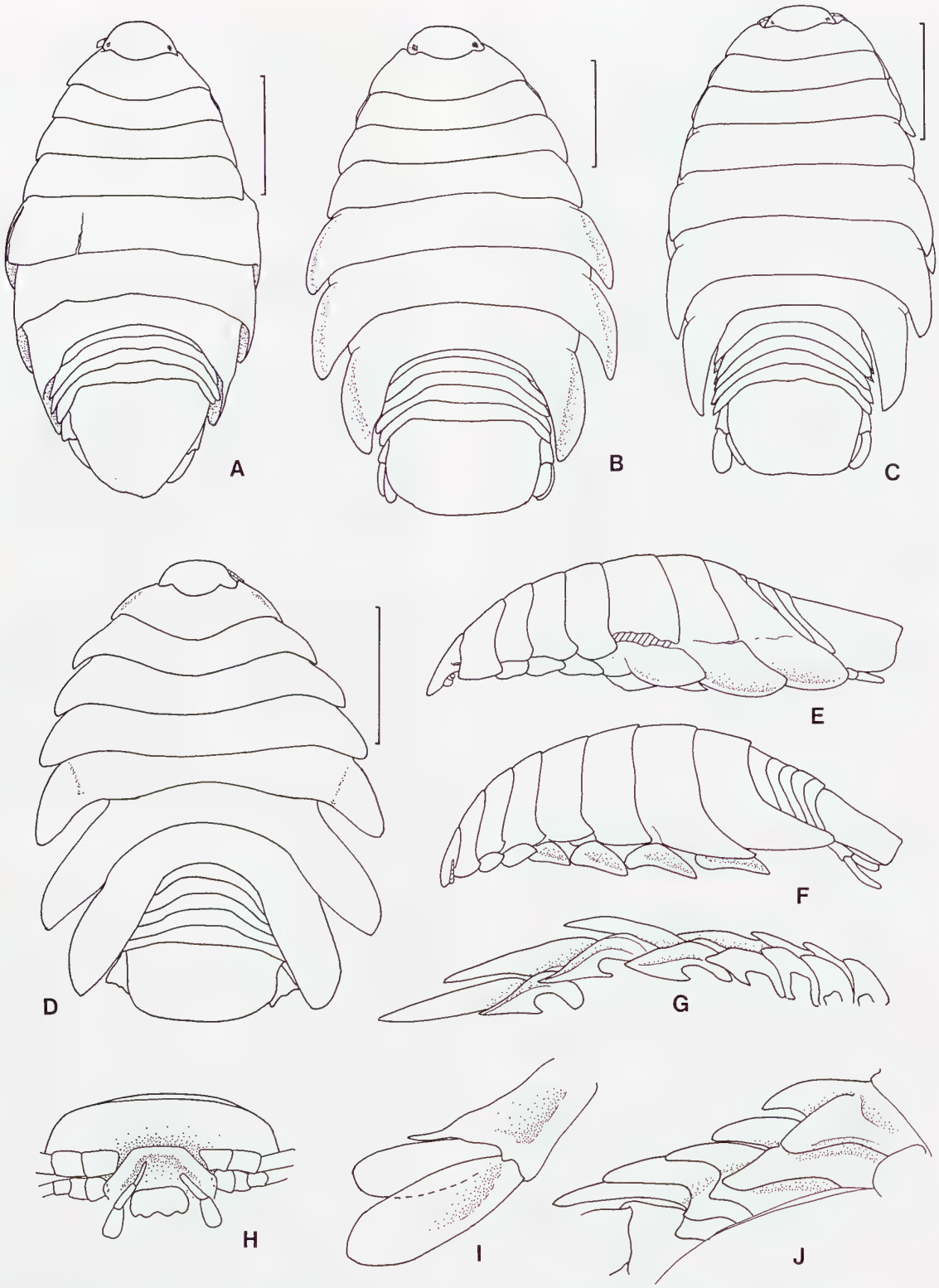

Fig. 23. *Creniola laticauda.* **A,** holotype; **B,** female, AM P19583; **C,** female, NMV J11571; **D,** female, AM G1799; **E,** holotype, lateral view; **F,** lateral view, NMV J11571; **G,** right coxae ventral view, SAM TC4481; **H,** frons NMV J11571; **I,** uropod, SAM TC4481; **J,** right pleonite, AM P19583. Scale lines 5.0 mm.

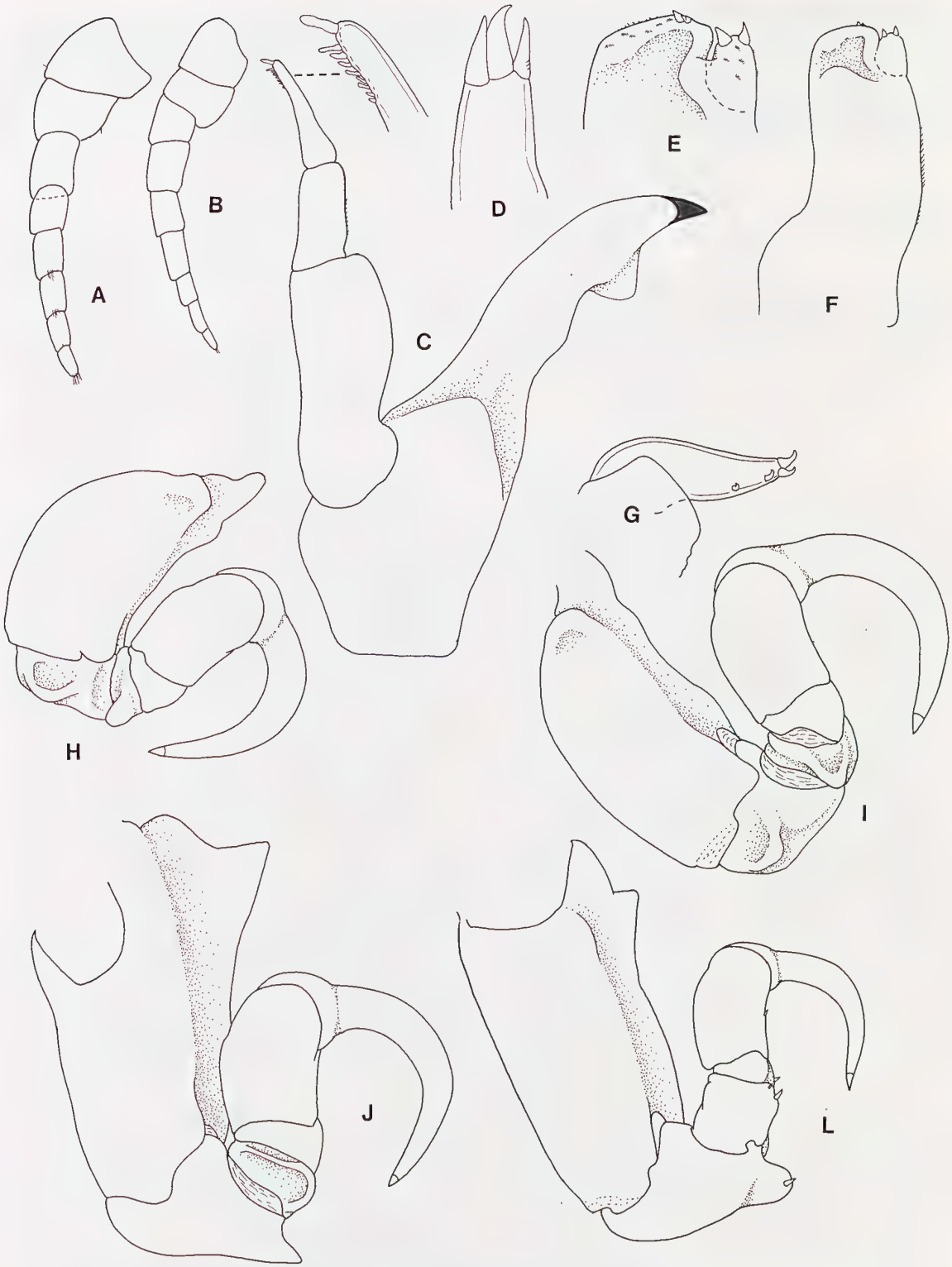

Fig. 24. *Creniola laticauda.* All SAM TC4481, except where indicated. **A,** antennule, female AM P19583; **B,** antenna, AM P19583; **C,** mandible; **D,** maxilule apex; **E,** maxilla apex; **F,** maxilla; **G,** maxilliped article 3; **H–K,** pereopods 1, 2, 6, 7.

(SAM C285). Female, Kingston, no other data (SAM 284). Female, 80 km south of Cape Wiles, registered 1930, 137 m (AM E6758). Female, St Vincent Gulf, no data (SAM C1994). Female, off Venus Bay, SA, June 1982, 33—46 m, coll. S. Doyle (SAM TC4480). Western Australia: female, 110 km southeast of Eyre, 33°04′S, 127°12′E, 1 Aug 1981, depth 96 m, coll. CSIRO, FRV *Soela* (SAM TC4483). Female, Albany, 10 Mar 1923, on fish (WAM 590-86). Male, Albany, no date, on stingray, with label WAM 836-39 (WAM 1263-85). Female, Esperance Bay, 9 Sept 1978, 55 m (WAM 1259-85). Male, Torbay, near Albany, 9—13 June 1959, 36—56 m, in craypot, coll. B.K. Beaver on *Bluefin* (WAM 599-85).

Types. Holotype held at Museum National d'Histoire Naturelle, Paris, MNHN Is. 263.

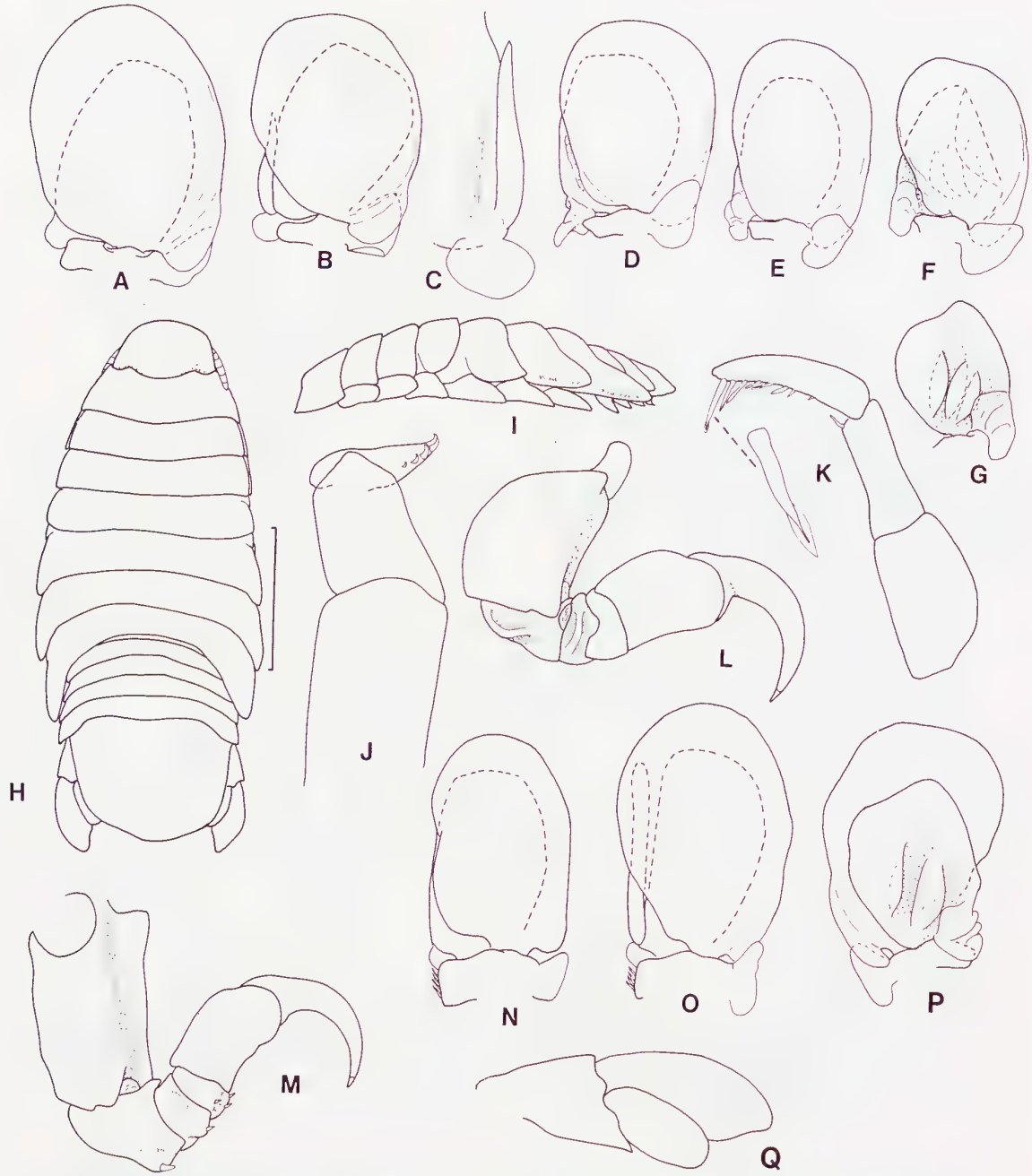

Fig. 25. *Creniola laticauda.* A—G, female SAM TC4481, remainder male, SAM C286. **A,** pleopod 1; **B,** pleopod 2; **C,** pleopod 2 endopod, proximomedial angle and appendix masculina; **D,** pleopod 3; **E,** pleopod 4; **F,** pleopod 5; **G,** pleopod 5 endopod, posterior view; **H,** dorsal view; **I,** pereon, pleon, lateral view; **J,** maxilliped; **K,** mandible palp; **L,** pereopod 1, **M,** pereopod 7; **N—P,** pleopods 1, 2, 5; **Q,** uropod. Scale line 3.0 mm.

Type locality. The label with the holotype gives only "Neue Hollande", but Schiödte & Meinert (1881) gave the locality as Westermann, Novae-Hollandiae. There is no such locality listed in Australian atlases or gazeteers. The type locality is therefore southeastern Australia as all of Schiödte & Meinert's (1881—1884) Australian material came from localities between Adelaide, Hobart and Sydney.

Description of female. Body about 1.7 times as long as wide. Cephalon anterior margin subtruncate. Coxae posteriorly acute, not extending beyond posterior of segment; posterolateral angles of all pereonites posteriorly produced, those of pereonites 1—5 weakly so, 5 and 6 strongly produced. Pleonites all visible in dorsal view, all equal in width. Pleotelson short, subquadrate, about 0.67—0.73 as long as wide; posterior margin weakly rounded to medially indented.

Antennule and antenna extending to pereonite 1.

Mandible palp article 3 with 9 peg like spines along distolateral margin. Maxilliped article 3 with 4 recurved spines.

Pereopod 1 robust; merus with proximally directed boss; ischium with posterolateral ridge; dactylus without nodules. Pereopods 2 and 3 similar to pereopod 1. Pereopod 6 basis with prominent anterolateral carina, proximal angle of which is acute; basis with posterodistal angle produced; merus with anteromedial margin with ridge; no spines present. Pereopod 7 basis with anterolateral carina; ischium posterodistal angle lobed, with single spine; merus with 2 spines on posterodistal margin; posterior margins of carpus and propodus each with single spine.

Pleopod 1 largely concealing pleopods 2—5; pleopod 2 appendix masculina with narrowing to point. Uropod exopod longer than endopod, both rami bluntly rounded; peduncle distomedial margin with narrowly produced process.

Male. Body about 2.3 times longer than wide. Appendages generally similar to female, but pleopod 1 not covering pleopods 2—5, appendix masculina longer; uropod exopod porportionally longer, extending beyond posterior of pleotelson.

Colour. In preserved specimen varies from pale tan to nearly black; always with 2 pale submedian longitudinal stripes running entire length of animal. Stripes may be wide, or so reduced as to be scarcely discernable.

Size. Ovigerous females 21.0—36.0 mm (mean 27.6, n=20); non-ovigerous females 18.0—25.0 mm (mean 18.4, n=7); males 11.5—15.5 (n=4, 2 male/female intermoult). The length/width for ovigerous females 1.44—2.08 mm (mean 1.70, n=19).

Variation. This species varies in the extent to which the posterolateral margins of the pereonites are produced, and to what extent the pleon is laterally overlapped by pereonite 7. The posterior margin of the pleotelson may be medially indented, straight or weakly rounded. One specimen (AM G1799) has the pereonites far more strongly expressed laterally than any other specimen. Pereopods and pleopods show little variation.

Remarks. The sculpture of the pereopods and shape of pereonite posterolateral margins readily identify this species. Data suggest that this is a sublittoral species occurring on fish that are associated with silty habitats.

Hosts. *Platycephalus* sp., *Zeus* sp., and "stingray". Hale (1926) recorded *Raja australis;* Hooper (1983) recorded a specimen from the head of *Platycephalus richardsonae.*

Distribution. At depths between 33 and 146 metres; Hooper (1983) recorded it from 300 metres. Southern coasts from Coffs Harbour, NSW, to Adelaide, SA (but no records from Tasmania), westward to Albany, WA.

Creniola saurida (Avdeev)

Figs 26—28

Nerocila saurida Avdeev, 1977: 139, fig. 1.

Material examined. Western Australia. North West Shelf, CSIRO F.R.V. *Soela* series: female (ovig 25.0), 19°30′S, 116°30′E, 12 May 1982, on *Spheroides,* depth 53 m, coll. NT Fisheries (NTM Cr2297); female (non-ovig 23.0), 20°00′S, 116°31′E, 4 Dec 1982, 55 m (NTM Cr4250); ?female (14.5), 19°03.5′S, 119°03.6′E, 28 Apr 1983, 80 m, coll. NTM (NTM Cr4530); female (ovig 27.0), 20°07′S, 116°47.8′E, 10 June 1983, depth 42—44 m, shelly sand, coll. G.C.B. Poore and H.M. Lew Ton (NMV J11183); female (ovig 21.0), 19°59.0′S, 117°51.7′E, 27 Aug 1983, coll T. Ward (WAM 2328-86); female (ovig 23.5), 19°04.0′S, 118°48.5′E, 28 Aug 1983, 84 m, coll. T. Ward (WAM 2329-86). Northern Territory: 2 females (ovig 25.0, non-ovig 20.0), Arafura Sea, 19 Oct 1981, 27 m, mud bottom, coll. H.K. Larsen (NTM Cr2288). Female (ovig 22.0), Arafura Sea, 19 Oct 1981, on *Hypodytes carinatus,* coll. A.J. Bruce (NTM Cr175). Queensland: female (ovig 25.5), Princess Charlotte Bay, Northern Qld, 23 Feb 1979, on *Spheroides multistriatus,* coll. AIMS, AM, QM (QM W8959). Female (ovig 24.5), southeast of Saint Helena Island, Moreton Bay, 24 Nov 1981, depth 18—22 m, coll. R.C. Willan (QM W10411). Female (ovig 19.0 mm), Moreton Bay, 31 Mar 1975, on "goatfish" (QM W12196). Female (ovig 30.5), Moreton Bay, Nov 1981, on *Saurida tumbil,* coll. Ebenezer Adjei (QM W10268). New South Wales: female (21.0), Sandon River, 12 Dec 1980, on stingray, coll. B. Ingram (AM P37163). 5 females (ovig ca. 18.0, 18.0, 22.5, 29.0, non-ovig 22.5) northeast of Yamba, 29°21′S, 153°29′E, 21 Mar 1985, 50 m, coll. FRV *Kapala,* (AM P37154).

Additional material. Female, North West Shelf, 19°30′S, 116°30′E, 12 May 1982, 53 m, coll. L. Bullard (NTM Cr2297). Female, Arafura Sea, 10°28′S, 132°10′E, 19 Oct 1981, 27 m, coll. H.K. Larson on FV *Anson* (NTM Cr2288). Female, east of Tully, Qld., 18°05′S, 147°03′E, 18 Jan 1986, on *Satyrichthyes welchi,* 220 m, coll. H.K. Larson on FRV *Soela* (NTM Cr3624). Female, off Malabar, Sydney, 20 Nov 1973, 65 m, coll. A.M. Shelf Benthic Survey (AM P37164).

Types. Institute of Oceanography, Vladivostok, U.S.S.R. Catalogue numbers 75050 and 75051 (Avdeev, 1977).

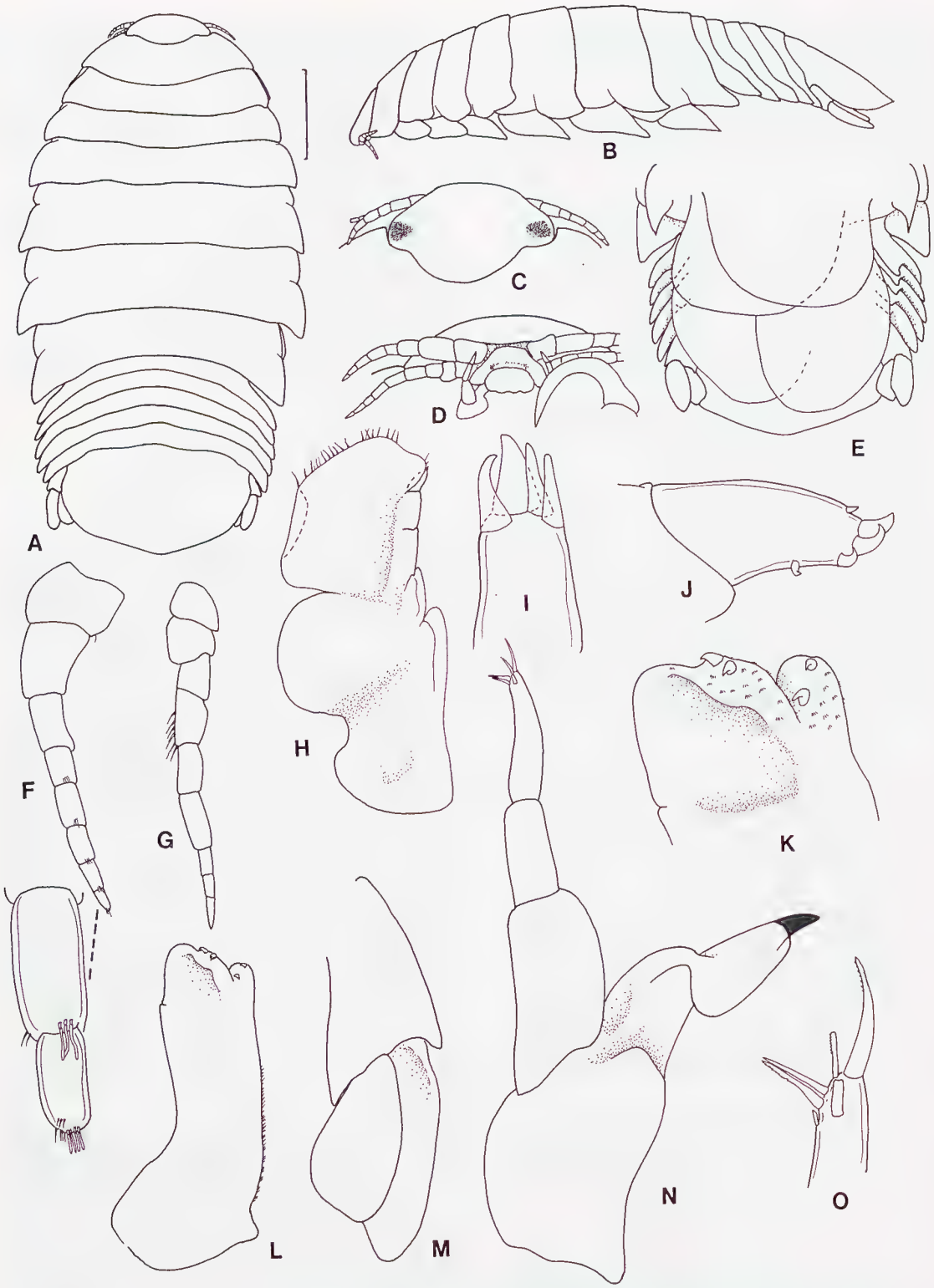

Fig. 26. *Creniola saurida.* All female QM W10268. **A,** dorsal view; **B,** lateral view; **C,** cephalon; **D,** frons; **E,** pleon, ventral view; **F,** antennule; **G,** antenna; **H,** maxilliped; **I,** maxillule apex; **J,** maxilliped article 3; **K,** maxilla apex; **L,** maxilla; **M,** uropods; **N,** mandible; **O,** mandible palp, apex. Scale line 5.0 mm.

Type locality. Northwestern coast of Australia (Avdeev, 1977).

Description of female. Body about 2.0 times as long as wide. Cephalon anterior margin rounded; eyes with facets indistinct. Coxae scarcely visible in dorsal view, becoming progressively more acute towards posterior; never extending posterior to segment. Posterolateral angles of pereonites 5—7 weakly produced. Pleonites all visible, pleon 0.87 width of pereonite 6. Pleotelson very short, 0.58—0.68 as long as wide; posterior margin wide, shallowly angled to obscure median point.

Antennule and antenna both extending to pereonite 1.

Mandible palp article 3 with 6 terminal setae. Maxilliped article 3 with 3 long recurved spines and 2 small spines.

Pereopod 1 dactylus strongly curved; pereopod 2, 3 and 4 similar to 1, but becoming progressively longer. Pereopod 6 with one single spine on merus, carpus and propodus. Pereopod 7 with prominent spines on posterior margins of ischium to propodus.

Pleopod 2 endopod with faint fold.

Uropod rami not extending to posterior of pleotelson, exopod longer than endopod, apex broadly rounded; endopod broadest distally, distinct angles rounded.

Male. Not Known.

Colour. In life, salmon pink; in alcohol pale tan to pink.

Size. Ovigerous females 18.0—30.5 mm (mean 21.8, n=14); non-ovigerous females 14.5—23.0 mm (mean 20.0, n=4).

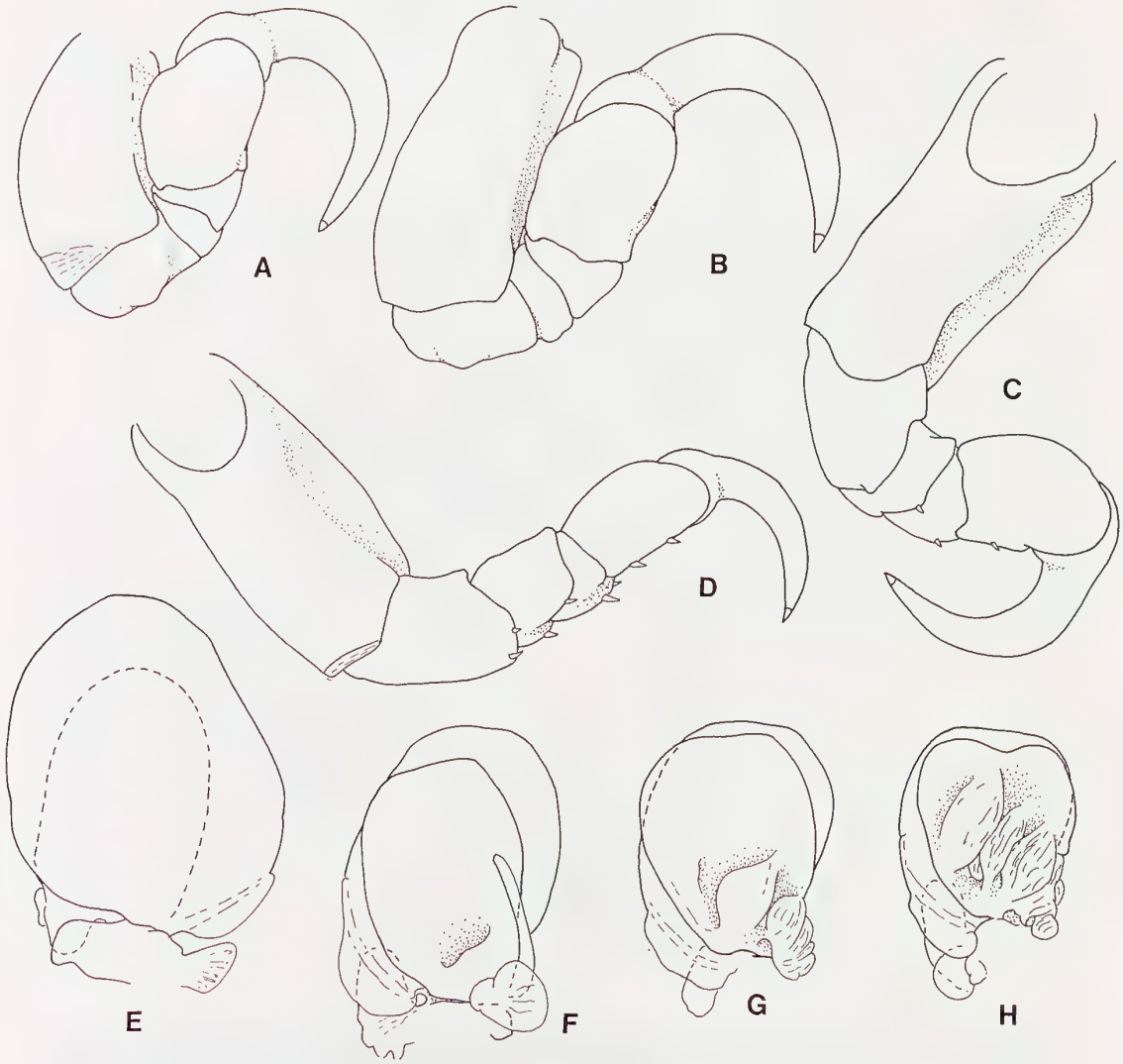

Fig. 27. *Creniola saurida.* All female QM W10268. **A—D,** pereopods 1, 2, 6, 7; **E—H,** pleopods 1, 2, 4, 5.

Variation. The smallest specimen had longer spines on pereopod 7 and maxilliped article 3, and a slightly longer appendix masculina, but did not otherwise differ from females. The shape of the posterior margin of the pleotelson varies from subtruncate (Fig. 28F) to weakly produced (Fig. 26A).

Remarks. This species is easily recognised by the short coxae, lack of pereonite extensions and the very short pleotelson. The types of *Crenolia saurida* were not made available for study. It is possible to identify the present material from Avdeev's (1977) illustrations, the short coxae and wide pleon being unique to this species.

Creniola saurida occurs commonly in trawl catches, and occurs on fish that are sedentary soft bottom dwellers.

Hosts. *Saurida tumbil, Hypodytes carinatus, Spheroides multistriatus, Satyrichthyes welchi.*

Distribution. North West Shelf, WA; Northern Territory; Princes Charlotte Bay, Moreton Bay, Qld; off Yamba, to depth of 220 m, and off Sydney, NSW.

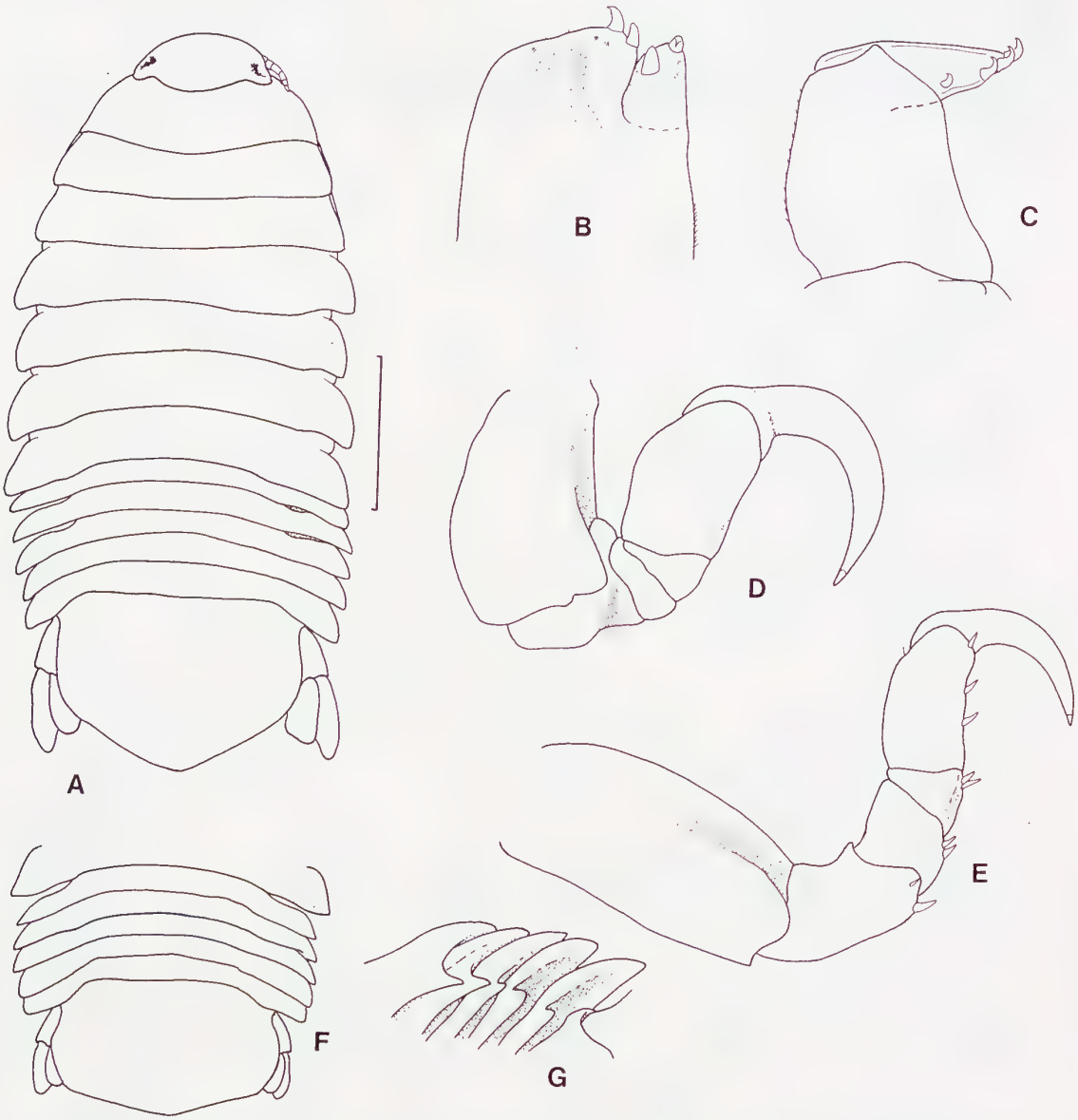

Fig. 28. *Creniola saurida.* A—F, ?male, 14.5 mm, NTM Cr4530. **A,** dorsal view; **B,** maxilla apex; **C,** maxilliped article 3; **D,** pereopod 1; **E,** pereopod 7; **F,** female (non-ovig 22.5), off Yamba, NSW (AM P37154); **G,** female (ovig 29.0), off Yamba (AM P37154), ventral view of left pleonites. Scale line 3.0 mm.

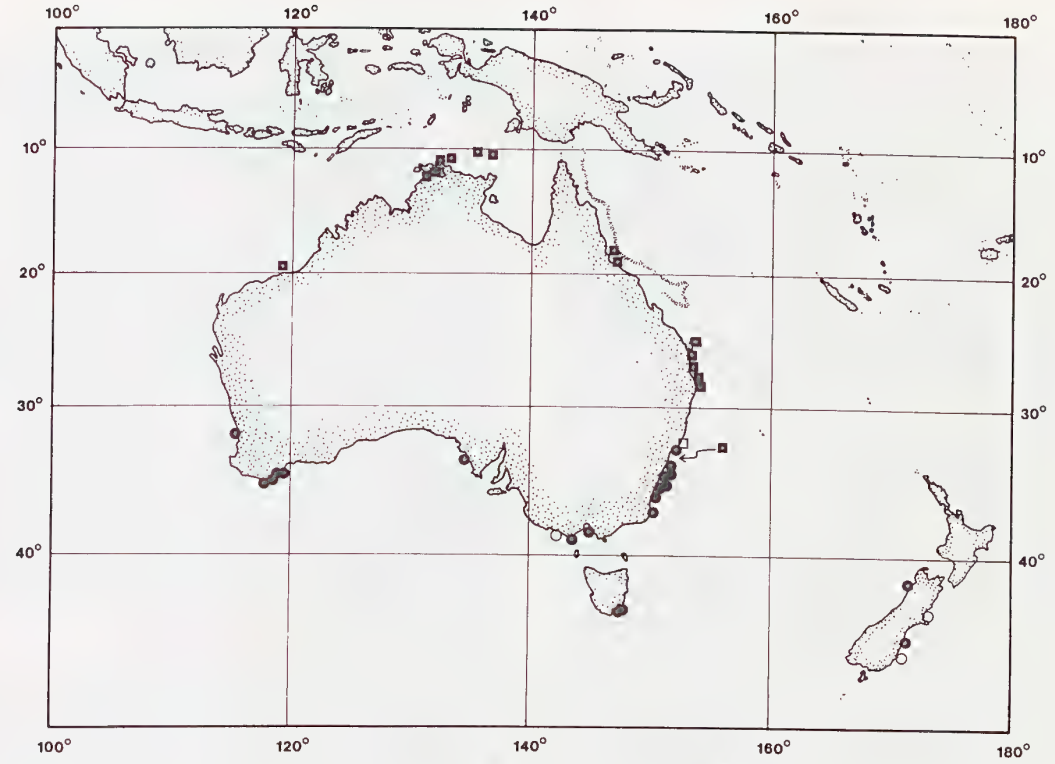

Fig. 29. Australian distribution of *Nerocila orbignyi* (●) and *Nerocila monodi* (■). Open symbol denotes literature record.

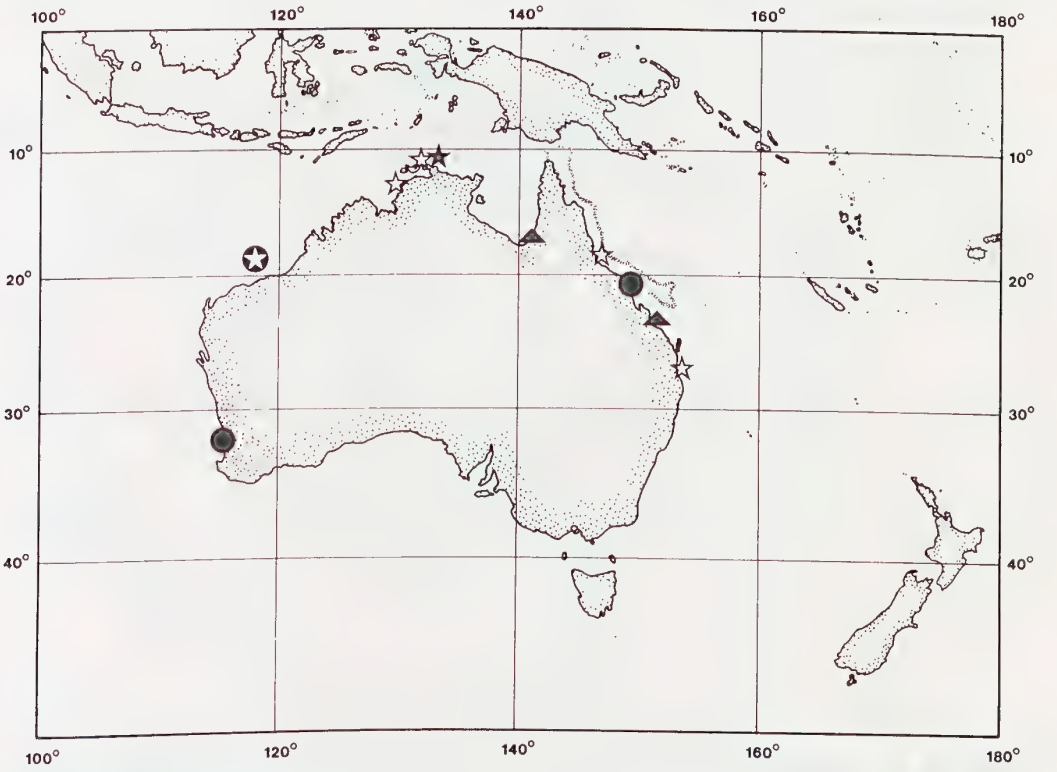

Fig. 30. Australian distribution of *Nerocila* sp. (✪), *Nerocila congener* (★), *Nerocila phaiopleura* (●), *Nerocila barramundae* (▲), *Nerocila lomatia* (☆).

Annotated list of names within *Nerocila*

This list gives the original description, the most recent publication giving a full synonymy and, in some instances, a full synonymy. Comments are given on the current status of the name, and on the need of redescription. Of the following four species formerly placed in *Nerocila, N. laticauda, N. breviceps* and *N. saurida* are now placed in *Creniola* and *N. schadleri* Nierstrasz is transferred to *Amblycephalon* Pillai, 1954 (Pillai, 1967). Unless otherwise indicated, assessments have been made from the literature. Where type specimens have been examined, the catalogue number is given. (* Indicates species unrecognisable from existing descriptions.)

1. **N. aculeata* Dana, 1853. *Nomen dubium,* present study.
2. **N. aculeata* Milne Edwards, 1840. *Nomen dubium.* The locality for this specimen is the Indian Ocean, and the type specimen is held at MNHN (Is. 237). Unfortunately nothing but fragments and debris remain, and the identity of this species can never be established.
3. *N. acuminata* Schiödte & Meinert, 1881. Specimens examined at the USNM and BMNH. An East Pacific and Caribbean species (Brusca, 1981), it belongs to the *N. orbignyi* group of species. In some specimens the uropod shape (Fig. 33A–C) approaches that of *N. orbignyi.* Nunomura's (1981) record from Japan is probably of *Nerocila japonica.*
4. *N. adriatica* Schiödte & Meinert, 1881. Synonym of *N. orbignyi,* present study.
5. *N. affinis* Milne Edwards, 1840. Synonym of *N. orbignyi,* present study.
6. *N. armata* Dana, 1853. Synonymy: *Nerocila armata* Dana, 1853: 761, pl. 50, figs 10a–d.—Gerstaecker, 1882: 274; Monod, 1931: 6, figs 2, 4; 1937: 465; Nierstrasz, 1931: 125; Van Name, 1940: 123, 135; Brian & Dartevelle, 1949: 136, figs 11, 12; 1975a: 330, pl. 3, figs 23, 25; Moreira & Sadowsky, 1978: 100, 110, 116; Rockiki, 1984: 106, figs 26; Trilles, 1986: 620 (citation).

Nerocila rhabdota Koelbel, 1879: 409, pl. 2, figs 2a–c.—Schiödte & Meinert, 1881: 39, pl. 2, figs 5, 6; Gerstaecker, 1882: 182; Monod, 1924: 79, fig. C, p. 76, Figs A,B, p. 80; Van Name, 1920: 43, 57, figs 10, 11; Trilles & Raibut, 1971: 71, 81, pl. 3, photo. 1; 1973: 273, 276, 280; Rockiki, 1984: 100, figs 24, 25; Trilles, 1986: 620.

Uncertain identity: Szidat, 1948: 46; 1955: 216.

Material examined. 4 females (ovig 21.5, 16.0, 15.5, 14.0), Birakiri, Bonny River, Nigeria, 4°34.2′N, 7°08.0′E, 15–20 Dec 1985, 15 km N.N.W. of Bonny Town, no host, coll. C.B. Powell and B. Olaobesikan (USNM 231175). Female (ovig 25.0), Sierra Leone

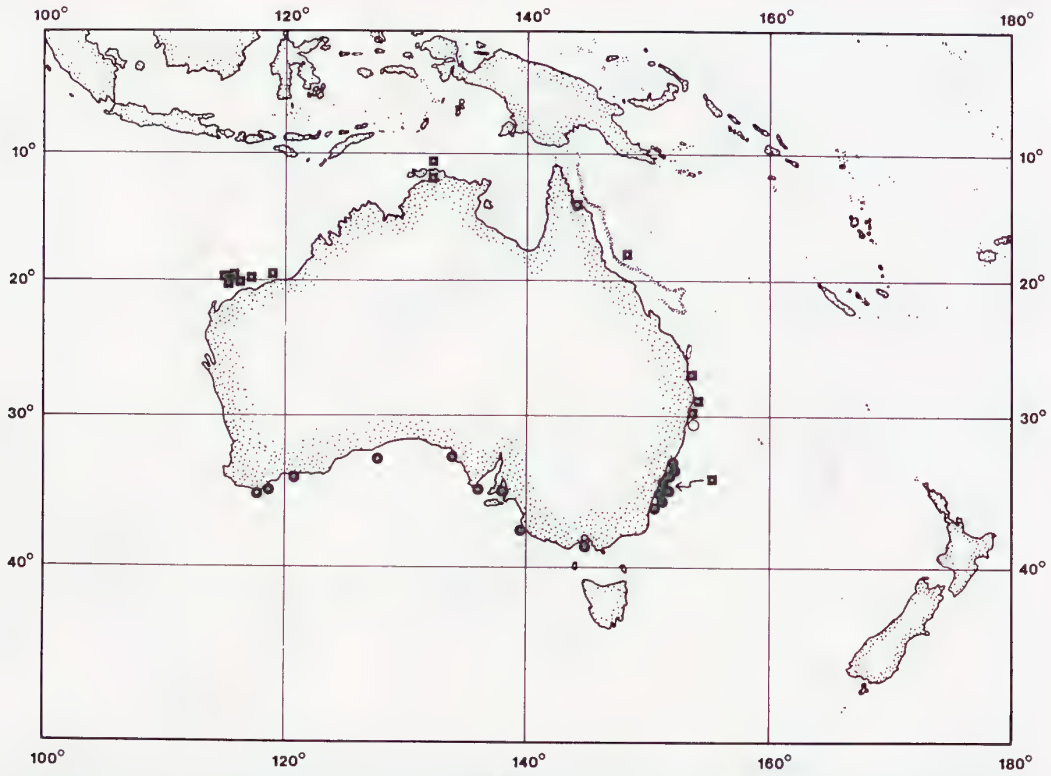

Fig. 31. Australian distribution of *Crenolia laticauda* (●) and *Crenolia saurida* (■). Open symbol denotes literature record.

River, 6 June 1953, on tail of *Otolithus macrognathus,* coll. WAFRI (BMNH 1963:3:10:6). Female (ovig 15.0) Bagru River, West Africa, 29 Dec 1952, coll. WAFRI (BMNH 1963:3:10:26).

Accepted as valid, although Dana (1853) recorded the species only from Rio de Janeiro. First revised by Monod (1931), material that corresponds to Monod's *N. armata* originates solely from West Africa, and it is unclear whether Monod's material is the same as that recorded by Dana. Dana's specimens are not extant, and it is unlikely that this problem can be resolved. Additional figures provided here (Fig. 33D—K); the species is best recognised by acute coxae 2 and 3 and the long uropods.

Trilles' (1973c) record of *N. armata* is not that species, but *N. orbignyi.* Trilles' figure (pl. 3, fig. 4) is of a specimen from Cameroon later identified and figured by Trilles (1975a) as *N. fluviatilis.* Trilles (1977) recorded *N. armata* from the Canary Islands. These specimens (RMNH 3980) are not *N. armata* sensu Monod (1931) as used here, but appear closest to *N. acuminata* or *N. orbignyi.*

7. *N. australasiae* Schiödte & Meinert, 1881 (MCZ 1139). Synonym of *N. orbignyi,* present study.

8. *N. bartschii* (Boone, 1918). Synonym of *N. acuminata.*

9. *N. bivittata* (Risso, 1816). Widely distributed Mediterranean species (Trilles, 1975b, 1977).

10. *N. blainvillii* Leach, 1818. Type species of the genus, which has never been fully described or figured. Examination of the types (BMNH 1979:400:2) show that it appears not to differ from *N. bivittata.* Additional figures provided (Fig. 34A—D).

11.**N. brasiliensis* Dana, 1853. *Nomen dubium,* present study.

12. *N. breviceps* Schiödte & Meinert, 1881. Here transferred to *Creniola.* Additional figures of the holotype (MCZ 1079) are provided (Fig. 32).

13.**N. brongnarti* (Risso, 1816). *Nomen dubium,* the description allows no assessment to be made of the species or genus.

14.**N. burtiasi* Belloc, 1929. Belloc (1929) provides a

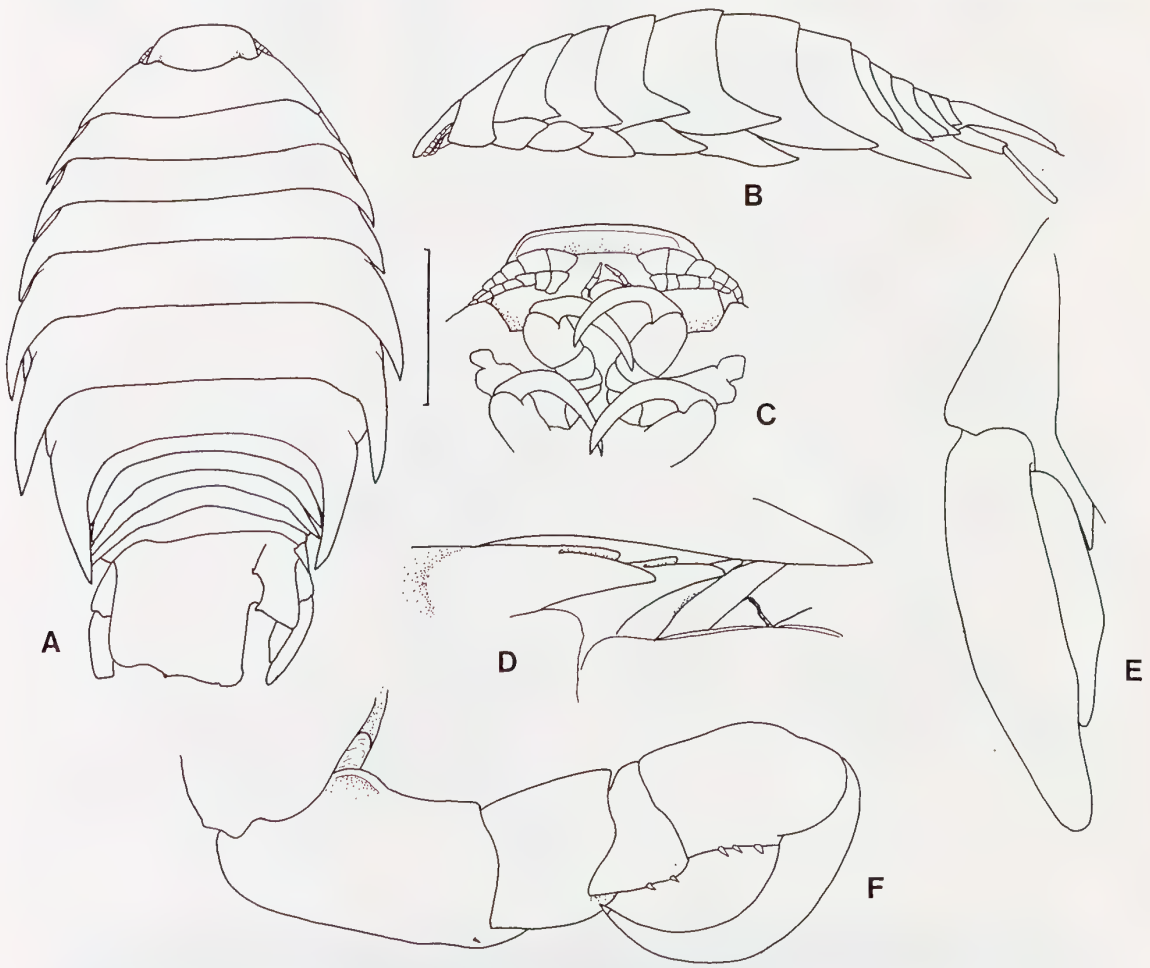

Fig. 32. *Creniola breviceps.* All figs of holotype (MCZ 1079). **A,** dorsal view; **B,** lateral view; **C,** ventral view, cephalon; **D,** ventral view, left pleonites; **E,** uropod; **F,** pereopod 7. Scale line 5.0 mm.

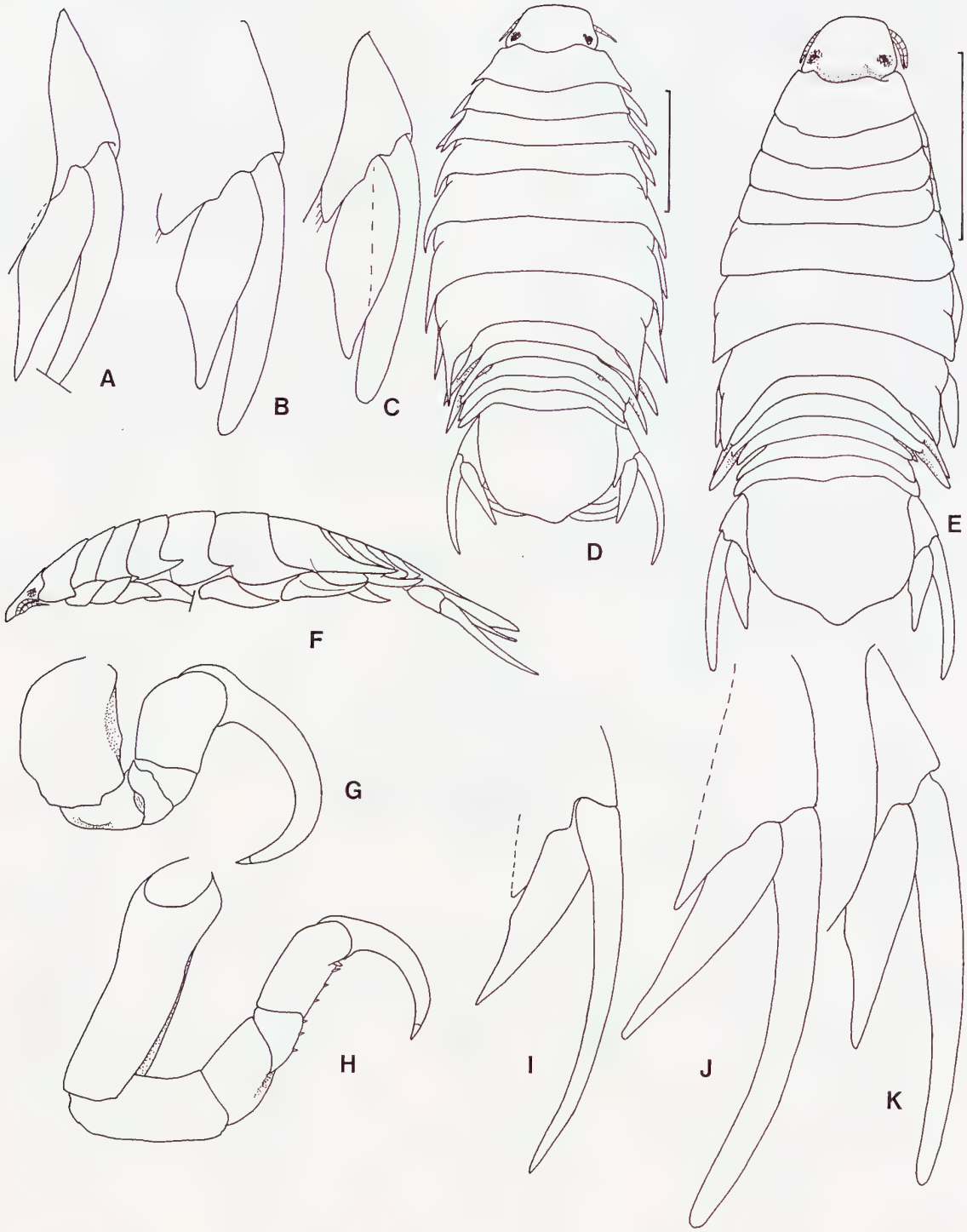

Fig. 33. *Nerocila acuminata:* **A,** right uropod, female (ovig 22.0) and **B,** right uropod, female (non-ovig 19.0), Pacific Panama (USNM 86436); **C,** right uropod, female (18.0), Louisiana, Gulf of Mexico (USNM 187036). *Nerocila armata,* all Bonny River, Nigeria (USNM 231175) except where indicated: **D,** dorsal view, female #1, 21.0; **E,** dorsal view, female #2, 16.0; **F,** female #1, lateral view; **G,** pereopod 1, female #1; **H,** pereopod 7, female #1; **I,** left uropod, ventral view (BMNH 1963.3.10.6); **J,** right uropod, female #1; **K,** right uropod, female #2. Scale lines 5.0 mm.

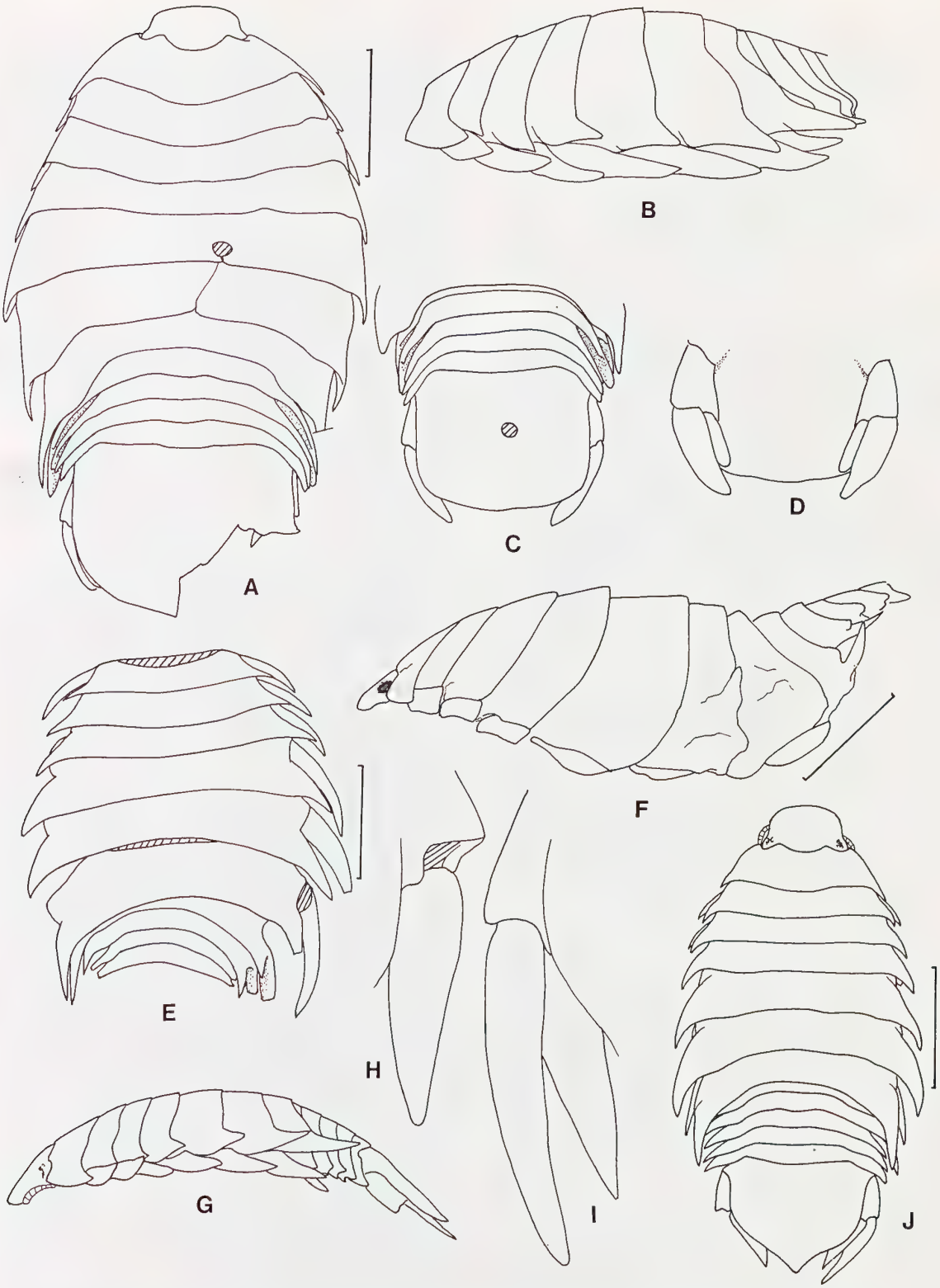

Fig. 34. *Nerocila blainvilli*, syntypes: **A,** dorsal view; **B,** pereon and pleon, lateral view; **C,** pleon and pleotelson, broken syntype; **D,** ventral view of uropods, broken syntype. *Nerocila depress*: **E,** holotype. *Nerocila excisa:* **F,** holotype. *Nerocila japonica,* holotype: **G,** lateral view; **H,** right uropod, ventral view; **I,** left uropod, ventral view; **J,** dorsal view. Scale lines 5.0 mm.

figure which he attributes to Acloque (1899). Validity of the species is uncertain.
15. *N. californica* Schiödte & Meinert, 1881. Synonym of *N. acuminata.*
16. *N. cebuana* Schiödte & Meinert, 1881. Synonym of *N. congener,* present study.
17. *N. cephalotes* Schiödte & Meinert, 1881. Synonym of *N. orbignyi,* present study.
18. *N. congener* Miers, 1880. Australia and Philippines, present study.
19. *N. ctenophora* (Koelbel, 1879). Synonym of *N. sundaica* (see Bowman, 1978).
20.**N. cuspidata* Costa, 1851. *Nomen dubium.*
21. *N. depressa* Milne Edwards, 1840. Philippines, Indo-China to Bombay, India (Trilles, 1975a, 1979). The type locality is not known. The specimen at the MNHN (Is. 508), believed to be the type specimen (Fig. 34E), is in very poor condition.
22. *N. dolichostylis* Koelbel, 1879. Synonym of *N. depressa;* examination of the holotype (NMW 5279).
23. *N. excisa* (Richardson, 1901). Holotype (Fig. 34F) USNM 46435. Parasitic on pelagic fishes in the central and East Pacific (Trilles, 1972; Brusca, 1981).
24.**N. exocoeti* Pillai, 1954. No adequate description exists for this species. Known only from India.
25.**N. falcata* (Fabricius, 1787). No adequate data exists for this species. See comments under 'Type species' for *Nerocila.*
26. *N. falklandica* Cuningham, 1871. The type specimen is immature and cannot be related to adults of the *N. orbignyi* complex of species. Here regarded as *species inquirenda.* Holotype BMNH 1985:266:1.
27. *N. fluviatilis* Schiödte & Meinert, 1881. Synonymy: *Nerocila fluviatilis* Schiödte & Meinert, 1881: 66, pl. 5, figs 6—9.—Gerstaecker, 1882: 474; Van Name, 1936: 31, 431, fig. 267; Cordero, 1937: 3, 4, figs 1—8, photo. 1a, b; Szidat, 1948: 45; 1955: 216; 1965: 84; 1966: 3; Teodoro, 1972: 141; Moreira & Sadowsky, 1978: 100, 110, 117; Bowman, 1978: 35.
Uncertain identity: Behre, 1950: 371.

Material examined. Female (ovig 21.0), male (15.0), St. Antonio, Angola, Aug 1915, coll. Land and Chaplin (part of material reported on by Van Name, 1920) (USNM 63640). Female (ovig 25.0) Rio de la Plata, Banco Ingles, Argentina, 29 Dec 1925, on *Lagenichthyes ancylooom,* no other data (USNM 233396). Female, River Plata, South America (BMNH 1928:12:1:907). Female (ovig 28.0), Punta del Diablo, Uruguay, Feb 1971, from "pejerry" (Atherinidae) (USNM 231181); female (30.0), male (16.0), as previous, but 17 Jan 1971, on "neck" of *Pontoporia blainvillei* (USNM 231179); all coll. R.L. Brownell Jr. Also the following material from Uruguay: USNM numbers: 42182 (Montevideo); 42383 (Mar del Plata); 57125; 61438; 61447; 65782 (Grand Island); 86440 (coast of Maldravado). BMNH numbers: 1956:10:10:39 (Montevideo); 1903:9:30:4 (Montevideo, harbour).

Recorded along the coasts of Argentina and Uruguay with one specimen examined here from Angola, Africa. Additional figures are provided here (Fig. 35E—I). The species can be recognised by the sinuate uropodal endopod with a prominent medial tooth. Van Name (1936) gives evidence that the species is primarily marine. Syntypes are held at the MCZ and the ZMC (Schiödte & Meinert, 1881). Trilles' (1975a) record of this species is of *N. orbignyi,* the uropods of his specimen readily identify the species.
28.**N. heterozota* Ahmed, 1970. Arabian Gulf. The figures and description are inadequate, and do not allow assessment of the species.
29. *N. japonica* Schiödte & Meinert, 1881. Japanese waters. Additional figures of the holotype (NRM 4975) are provided (Fig. 34G—J); the species can be recognised by the acute, smoothly tapered uropodal endopod.
30. *N. kisra* Bowman & Tareen, 1983. Kuwait.
31. *N. laevinota* Miers, 1880. Examination of types (BMNH 1880:6) show this to be a synonym of *N. sundaica.*
32.**N. lanceolata* (Say, 1818). Georgia, U.S.A. (Richardson, 1905), inadequately known.
33.**N. lata* Dana, 1853. These were probably lost with the sinking of the sloop *Peacock.* As the figures are inadequate, this species is best regarded as *nomen dubium.*
34. *N. laticauda* Schiödte & Meinert, 1881. Transferred to *Creniola,* present study.
35. *N. laticeps* Bovallius, 1887. Synonym of *N. orbignyi,* present study.
36.**N. latiuscula* Dana, 1853. *Nomen dubium,* present study.
37.**N. livida* Budde-Lund, 1908. Zanzibar, inadequately described and of uncertain identity; I have not located the type material.
38. *N. longispina* Miers, 1880. Malaysia; has never been figured, and figures of the holotype given here (Fig. 35A—D). *Nerocila longispina* belongs to the *Emphylia* group of species, and is the only species of that group, other than *N. sundaica,* that has the anterior margin of the cephalon narrowly rounded and the antennule bases close set. It differs from *N. sundaica* in having the uropod endopod lateral margin finely serrate, and the posterior coxae more strongly angled away from the body.
39. *N. loveni* Bovallius, 1887. Indonesia (Trilles, 1979); I have not located the type material.
40. *N. macleayii* Miers, 1884. Synonym of *N. orbignyi,* present study.
41.**N. madrasensis* Ramaskrishna & Venkata Rao, 1978. Possibly related to *N. trichiura,* the description precludes assessment of the status of this species. Known only from India.
42. *N. maculata* Milne Edwards, 1840. Synonym of *N. orbignyi,* present study.
43. *N. monodi* Hale, 1940, present study.
44.**N. munda* Harger, 1878. Inadequately known, and of uncertain identity. Specimens in the USNM

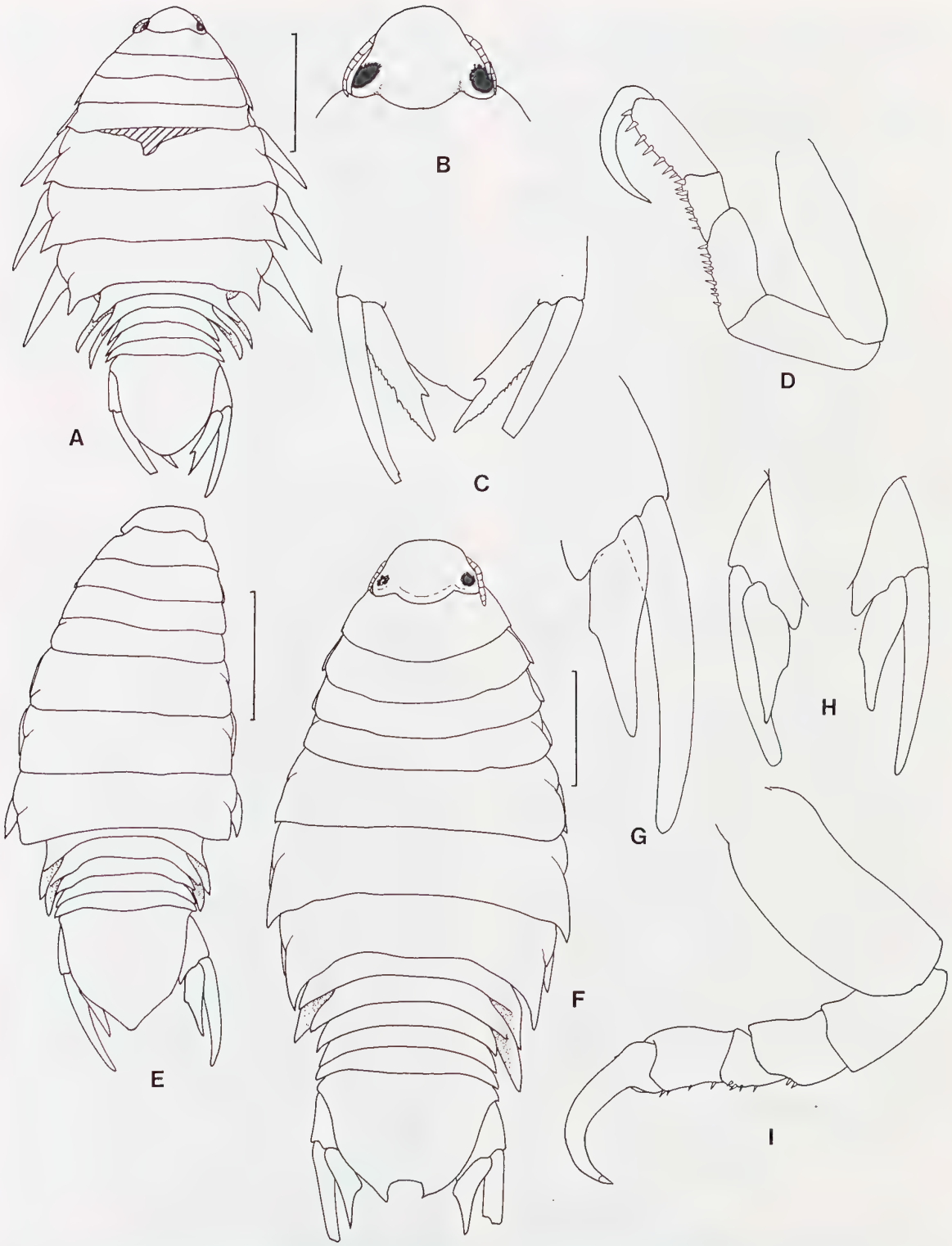

Fig. 35. *Nerocila longispina,* holotype: **A,** dorsal view; **B,** cephalon; **C,** uropods, ventral view; **D,** pereopod 7. *Nerocila fluviatilis:* **E,** female (ovig 21.0), Angola (USNM 63640); **F,** female #1, Uraguay (USNM 231181); **G,** right uropod, Angola female; **H,** right and left uropod; female (26.0), Uraguay (USNM 42383); **I,** pereopod 7, Angola female. Scale lines 5.0 mm.

identified as *N. munda* are a species of *Lironeca.* Reported from the Atlantic coasts of the U.S.A.
45. *N. neapolitana* Schiödte & Meinert, 1881. Synonym of *N. orbignyi,* present study.
46. *N. novaezelandiae* Schiödte & Meinert, 1881. Synonym of *N. orbignyi,* present study.
47. *N. saurida* Avdeev, 1977. Transferred to *Creniola,* present study.
48. *N. schadleri* Nierstrasz, 1915. Transferred to *Amblycephalon,* present study.
49. *N. sundaica* Bleeker, 1857. Widely distributed Indo-Pacific species (Bowman, 1978).
50. *N. phaiopleura* Bleeker, 1857. Present study.
51. *N. philippinensis* Bovallius, 1887. Synonym of *N. congener,* present study.
52.**N. pigmentata* Bal & Joshi, 1959. Synonymised with *N. depressa* by Trilles (1975a).
53.**N. pulicatensis* Jayadev Babu & Sanjeera Raj, 1980. Quoted in Parimala (1984); I have not been able to obtain a copy of the original description.
54. *N. recurvispina* Schiödte & Meinert, 1881. Recorded from Calcutta, India (holotype ZMB 3389).
55. *N. rogans* (Stebbing, 1924). Synonym of *N. orbignyi.*
56. *N. rhabdota* Koelbel, 1879. Synonym of *N. armata,* Trilles, (1975a), and present study.
57. *N. serra* Schiödte & Meinert, 1881. Widespread Indo-Pacific species, but not well known. One syntype (NRM 4974) refigured by Bowman & Tareen (1983).
58. *N. sigani* Bowman & Tareen, 1983. Kuwait.
59.**N. tartowskii* Popov, 1933. Black Sea, status uncertain; Popov's figures show no differences from *N. orbignyi,* and the species is included in the synonymy for *N. orbignyi.*
60.**N. tenuipes* Dana, 1853. *Nomen dubium,* present study.
61. *N. trailli* Filhol, 1887. Synonym of *N. orbignyi,* present study (holotype MNHN Is. 553).
62. *N. trichiura* (Miers, 1877). Holotype BMNH 1846:104. Parasitic on flying fishes. Atlantic and Indian Oceans (Trilles, 1975a).
63. *N. trivittata* Milne Edwards, 1840. The status of this species is currently in question. Trilles (1979) believes it to be the senior synonym of *N. serra,* but Bowman & Tareen (1983) do not accept that opinion. I believe that *N. trivittata* is best regarded as *nomen dubium.*
64. N. vittata Lucas, 1849. Synonym of *N. orbignyi,* present study.

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References

* not seen by author

*Acloque, A., 1899. Faune de France — Thysanoures, Myriopodes, Arachnides, Crustacés, Némathelminthes, Lophostomes, Vers, Mollusques, Polypes, Spongiares, Protozoaires. J.B. Bailliere et Fils, Paris, 500 pp, 1664 figs.

Ahmed, M.M., 1970. New Isopoda (Flabellifera) from Iraq and Arabian Gulf, IV. *Nerocila heterozota* sp. nov. Bulletin of the Iraq Natural History Museum 4: 55—57.

Amar, R., 1951. Isopodes marins de Banyuls. Vie et Milieu 2: 529—530.

Anon, 1957. Plymouth Marine Fauna. Marine Biological Association of the United Kingdom, Latimer Trend & Co. Ltd., Plymouth, 195 pp.

Avdeev, A.A., 1977. Three new species of parasitic isopods (Flabellifera, Anilocridae) from the collection of the Laboratory of Parasitology of Sea Animals of TINRO. Fisheries, Oceanography, Hydrobiology and Fish Parasitology of the Pacific Ocean 1011: 139—144.

Bal, D.V. & U.N. Joshi, 1959. Some new isopod parasites on fishes. Journal of the Bombay Natural History Society 56: 563—569.

Balcells, E., 1953. Sur des isopodes, parasites de poissons. Vie et Milieu 4: 547—552.

Barnard, K.H., 1914. Contributions to the crustacean fauna of South Africa. 3. Additions to the marine Isopoda, with notes on some previously incompletely known species. Annals of the South African Museum 10: 325a—442, pls 17—38.

——— 1925. Contributions to the crustacean fauna of South Africa. No. 9. Further additions to the list of Isopoda. Annals of the South African Museum 20: 381—410.

——— 1936. Isopods collected by the R.I.M.S. "Investigator". Records of the Indian Museum, Calcutta 38: 147—191.

——— 1940. Contribution to the crustacean fauna of South Africa. XII. Further additions to the Tanaidacea, Isopoda, and Amphipoda, together with keys for the identification of hitherto recorded marine and freshwater species. Annals of the South African Museum 32: 381—543.

*Behre, E.H., 1950. Annotated list of the fauna of the Grand Isle region. Occasional Papers of the Marine Laboratory, Louisiana State University, Baton Rouge, La 6: 1—66.

Belloc, G., 1929. Poissons de Chalut. Étude monographique du Merlu (*Merlucius merluccius* L.). Deuxième Partie. Revue des Travaux de l'Office des Peches Maritimes, Paris 2: 231—288.

Beneden, J.P., van, 1861. Recherches sur les Crustacés du littoral Belgique. Mémoires de l'Academie Royale du Belgique 33: 1—174, pls 1—21.

———— 1871. Les poissons des cotes de Belgique, leurs parasites et leurs commensaux. Mémoire de l'Academie Royale des Sciences, des Lettres et des Beaux Arts de Belgique 38: i—xx, 1—100, pls 1—6.

Berner, L., 1969. Les principaux Cymothoidés (Crustacés Isopodes) du Golfe de Marseille. Bulletin du Muséum d'Histoire Naturelle de Marseille 29: 93—95.

Beumer, J.P., L.D. Ashburner, M.E. Burbury, E. Jetté & D.J. Latham, 1982. A checklist of the parasites of fishes from Australia and its adjacent territories. Commonwealth Institute of Parasitology Technical Communication No. 48: i—vi, 1—99.

Bleeker, P., 1857. Recherches sur les Crustacés de L'Inde Archipélagique. II. Sur les Isopodes Cymothoadiens de L'Archipel Indien. Natuurkundige vereeniging in Nederlandsche-Indie, Batavia. Verhandelingen 2: 20—40, pls 1, 2.

Bolívar, J., 1892. Lista de la colección de crustáceos de España y Portugal del Museo de Historia Natural de Madrid. Actas de la Sociedad Española de Historia Natural 21: 124—141.

Bonnier, J., 1887. Catalogue des crustacés malacostracés recuellis dans al Baie de Concarneau. Bulletin Scientifique du Nord de La France et de la Belgique, 2 série, 10 Année 9—10: 36—422.

Boone, P.L., 1918. Descriptions of ten new isopods. Proceedings of the United States National Museum 54: 591—604.

Bovallius, C. 1887. New or imperfectly known Isopoda. Part III. Bihang till Kongelige Svenska Vetenskapsakademiens Handlingar 12, 4(4) 1—21, pls 1—4.

Bowman, T.E. 1978. Restoration of the subgenus *Emphylia* Koelbel for the parasitic isopod *Nerocila sundaica* Bleeker (Flabellifera, Cymothoidae). Crustaceana 34: 33—44.

Bowman, T.E. & I.U. Tareen, 1983. Cymothoidae of Kuwait (Arabian Gulf) (Crustacea: Isopoda). Smithsonian Contributions to Zoology 382: i—iii, 1—30.

Bragoni, R., B. Romestand & J.-P. Trilles, 1983. Parasitoses à cymothoadien chez le loup (*Dicentrarchus labrax* Linnaeus, 1758) en elevage. II. Écophysiologie parasitaire dans le cas de l'étang de Diana (Haute-Corse). Annales de Parasitologie Humaine et Comparée 58: 593—609.

Brian, A. & E. Dartevelle, 1949. Contribution a l'étude des isopodes marins et fluviatiles du Congo. Annales du Musée du Congo Belge. C. Zoologie, Série 1: 77—208.

Bruce, N.L., 1982. On a small collection of marine Isopoda (Crustacea) from Hong Kong. Proceedings of the first International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong, 1980. (B.S. Morton & K. Tseng, eds) 1: 315—324.

———— 1986. Revision of the isopod crustacean genus *Mothocya* Costa, in Hope, 1851 (Cymothoidae: Flabellifera), parasitic on marine fishes. Journal of Natural History 20: 1089—1192.

———— 1987a. Australian *Pleopodias* Richardson, 1910 and *Anilocra* Leach, 1818 (Isopoda: Cymothoidae), crustacean parasites of marine fishes. Records of the Australian Museum 39: 85—130.

———— 1987b. Australian *Renocila* Miers, 1880 (Isopoda, Cymothoidae), crustacean parasites of marine fishes. Records of the Australian Museum 39: 169—182.

Brusca, R.C., 1981. A monograph on the Isopoda Cymothoidae (Crustacea) of the eastern Pacific. Zoological Journal of the Linnean Society 73: 117—199.

Brusca, R.C. & E.W. Iverson, 1985. A guide to the marine isopod Crustacea of Pacific Costa Rica. Revista de Biologia Tropical 33 (Supplemento 1): i—iv, 1—77.

Budde-Lund, G., 1908. Isopoda von Madagascar und Ostafrika mit Diagnosen verwandter Arten. **In** Dr. A. Voelzkow, 'Reise in Ostafrika in der Jahren 1903—1905.' Wissenschaftlichen Ergebrisse 2: 263—308, pls 12—18.

Bullar, J.F., 1876. The generative organs of the parasitic Isopoda. Journal of Anatomy and Physiology 19(1): 118—123, pl. 4.

*Carus, J.V., 1885. Coelenterata, Echinodermata, Vermes, Arthropoda. Prodromus fauna Mediterranae, sive descriptio animalium Maris Mediterrenei incolarum quam comparata silva rerum quatenus innotuit odiectis locis et nominibus vulgaribus e orumque auctoribus in commodum Zoologorum, Vol. 1. E. Schweizerbatsche, Stuttgart, 525 pp.

Carvalho, R.N. de, 1944. Catálogo de coleccão de invertebrados de Portugal existentes no Museu Zoológico da Universidade de Coimbra. Memórias e Estudos do Museu Zoológico da Universidade de Coimbra 160: 1—15.

Chevreux, E., 1884. Crustacés Amphipodes et Isopodes des environs du Croisic. Comptes rendus de l'Association Francaises pour l'Avancement de Science, 12e session, Rowen (1883): 517—570.

Chilton, C., 1891. On the changes in form of a parasitic isopod *(Nerocila).* Transactions of the New Zealand Institute 23: 68—71, pl. 11.

———— 1911. The Crustacea of the Kermadec Islands. Transactions of the New Zealand Institute 43: 544—573.

———— 1926. Zoological results of a tour in the Far East. The Tanaidacea and Isopoda of Tale Sap. Records of the Indian Museum, Calcutta 28: 173—185.

Cordero, E.H., 1937. *Nerocila fluviatilis* y otros isópodos parásitos las familias Cymothoidae y Bopyridae del Uruguay y del Brasil. Anales del Museu de Historia Natural de Montevideo 2e serie 4: 3—11, 1 pl.

Costa, A., 1851. Caratteri di alcuni de'generi e specie nuove segrete nel presente catalogo. pp. 41—48, pl. 1. **In** F.W. Hope 'Catalogo dei crostacei Italiani e di molti altri de Mediterraneo, Napoli.'

Cunningham, R.O., 1871. Notes on the reptiles, Amphibia, fishes, Mollusca and Crustacea obtained during the voyage of H.M.S. 'Nassau' in the years 1866—69. Transactions of the Linnean Society of London 27: 465—502, pls 58, 59.

Dana, J.D. 1853. Crustacea, Part II. **In** 'United States

Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U.S.N.', Vol. 14. C. Sherman, Philadelphia, pp 689—1618. Atlas, pls 1—99, 1885.

Day, J.J., J.G. Field & M.J. Penrith, 1970. The Benthic fauna and fishes of False Bay, South Africa. Transactions of the Royal Society of South Africa 39: 1—108.

Desmarest, A.G., 1825. Considération générales sur la classe des Crustacés. Paris. pp xix + 446, 56 pls.

Dollfus, R.P., 1946. Essai de catalogue des parasites poisson-lune. Annales de la Société des Sciences Naturelles de la Charente-Maritime, Nouvelle Série 7: 68—76.

Dollfus, R.P., & J.-P. Trilles, 1976. A propos de la collection R.Ph. Dollfus, mise au point sur les Cymothoadiens jusqu'à present recoltés sur des Teléosteens du Maroc et de l'Algerie. Bulletin du Muséum National d'Histoire Naturelle 390, Zoologie 272: 821—830.

Dudich, E., 1931. Systematische und biologische Untersuchungen uber die Kalkienlagerungen des Crustaceenpanzers in polarisiertem lichte. Zoologica (Stuttgart) 30(80): i—ix, 1—54, pls 1—14.

Duvernoy, G.L., & Lereboullet, 1841. Essai d'une monographie des organes de la respiration de l'ordre des Crustacés isopodes. Annales des Sciences Naturelles, 2e série, Zoologie 15: 177—240.

Ellis, J., 1981. Some type specimens of Isopoda (*Flabellifera)* in the British Museum (Natural History) and the isopods in the Linnaean collection. Bulletin of the British Museum of Natural History (Zoology) 40: 121—128.

*Euzet, L., 1949. Contribution a l'étude de la faune du Bassin de Thau: l'etang des Eaux Blanches. Diplôme d'Études Supérieures, Montpelier, 76 pp, 2 figs.

*Fabricius, J.C., 1787. Mantissa Insectorum. I. Hafniae. 241 pp.

Filhol, H., 1885. Considerations relatives a la faune des Crustacés de la Nouvelle Zélande. Bibliotheque de l'École des Hautes Études, Section des Sciences naturelles, Paris 30(2): 1—60.

Fryer, G. & T.D. Iles, 1972. The cichlid fishes of the Great Lakes of Africa, their biology and evolution. Oliver & Boyd, Edinburgh; T.F.H. Publications, Neptune City, New Jersey, 641 pp.

Gerstaecker, A., 1882. Sechste Ordnung. Isopoda Asseln [Part], Pp. 97—278. **In** Dr. H.G. Bronn 'Klassen und Ordnung des Thier-Reichs, wissenschaftlich dargestellt in Wort und Bild.' Funfter Band II. Abtheilung. Gliederfussler: Arthropoda. Crustacea (Zweite Halfte: Malacostraca) 4, 5, 6, 7, 8. Leiferung.

Gibert i Olivé, A.M., 1920. Crustacis de Calunya. Treballs de Institució Catalana d'Historia Natural for 1919—1920: 9—128.

Gourret, P., 1907. Topographie, zoologique des Étangs de Caronte, de Labillon, de Berre et de Bolmon. Flore, Faune, Migrations, etc. Annales de Muséum d'Histoire Naturelle, Marseille, Zoologie 11: 1—166, pl. 1—3.

Guérin-Méneville, F.E., 1832. Crustacés. **In** 'Expédition scientifique de Morée, section des Sciences physiques.' III. 1re partie, Zoologie 2e section. Des animaux articules. Crustaces: 30—50.

——— 1835. Atlas. **In** 'Expedition scientifique de Morée, section des Sciences physiques. III.

Hale, H.M., 1926. Review of Australian isopods of the Cymothoid group. Part II. Transactions of the Royal Society of South Australia 50: 201—234, pls 26, 27.

——— 1929. The Crustaceans of South Australia. Part 2. Handbooks of the Fauna and Flora of South Australia. British Science Guild (South Australian Branch), Adelaide, pp 201—380.

——— 1940. Report on the cymothoid Isopoda obtained by the F.I.S. "Endeavour" on the coasts of Queensland, New South Wales, Victoria, Tasmania, and South Australia. Transactions of the Royal Society of South Australia 64: 288—304, pl. 18.

Harger, O., 1878. Report on the marine Isopoda of New England and adjacent waters. **In** 'The Report of the U.S. Commission of Fish and Fisheries, Part 6 1878: 297—462, pls 1—13.

Harrison, K., 1984. The morphology of the sphaeromatid brood pouch (Crustacea: Isopoda: Sphaeromatidae). Zoological Journal of the Linnean Society 82: 363—407.

Heller, C., 1866. Carcinologisch. Verhandlungen der Zoologisch-botanischen Gessellschaft in Wien 16: 723—760.

Hewitt, G.C. & P.M. Hine, 1972. Checklist of parasites of New Zealand fishes and their hosts. New Zealand Journal of Marine and Freshwater Research 6: 69—114.

Holthuis, L.B., 1978. Cymothoide isopoden van de Nederlandse kust en de Zuidelijke Noordzee. Bijdragen Faunisteit Nederland 5: 28—33, pl. 1.

Hooper, J.N.A., 1983. Parasites of estuarine and oceanic flathead fishes (Family Platycephalidae) from northern New South Wales. Australian Journal of Zoology, Supplementary Series 90: 1—69.

Hurley, D.E., 1961. A checklist and key to the Crustacea Isopoda of New Zealand and Subantarctic Is. Transactions of the Royal Society of New Zealand (Zoology) 1: 239—292.

Hutton, F.W., 1904. Index Faunae Novae Zealandiae. Philosophical Institute of Canterbury, N.Z., pp. viii + 372.

Huwae, P.H.M., 1977. De Isopoden van de Nederlandse Kust. Wetenschappelijke Mededelingen van der Koninklijke Nederlandse Natuurhistorische Vereniging 118: 1—44.

*Jayadev Babu, S. & P.J. Sanjeera Raj, 1980. Proceedings of the Symposium on Coastal Aquaculture 3: 820—823 (Quoted in Parimala, 1984).

Kensley, B., 1978. Guide to the marine isopods of southern Africa. South African Museum, Cape Town, 173 pp.

Koelbel, K., 1879. Ueber einige neue Cymothoiden. Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Klasse der Kaiserlichen Akademie der Wissenschaften 78(1): 401—416, pls 1, 2.

Kussakin, O.G., 1979. Marine and Brackish water isopod Crustacea. Suborder Flabellifera Akademy of Science, U.S.S.R. Leningrad, 470 pp. (in Russian).

Lagarrigue, J.G. & J.-P. Trilles, 1969. Nouvelles recherches écologiques sur les isopodes Cymothoidae Méditerranéens. I. L'importance, la calcification et les constituents organiques de la cuticle; ses variations suivant les espèces. Vie et Milieu ser. A 21: 117—136.

Latreille, P.A., 1802. Histoire naturelle des Crustacés et Insectes. Volumes 5, 6. Paris.

Leach, W.E., 1818. Cymothoidées. **In** 'Dictionnaire des Sciences Naturelle (F. Cuvier, ed.). Vol. 12: 338—354. Paris & Strasbourg.

Lincoln, R.J., 1971. Isopod fish parasites. The Marine

Observer 41(234): 184—186.
Lucas, P.H., 1846. Histoire naturelles des animaux articulés, par H. Lucas. Pt. 1 Crustacés, Arachnides, Myriapodes et Hexapodes. pp. xxv—403. **In** 'Exploration Scientifique de l'Algerie pendent les années 1840, 1841, 1842.' Paris, Imprimerie Nationale.
Mann, H., 1970. Copepoda and Isopoda as parasites of marine fishes. **In** 'A symposium on diseases of fishes and shellfishes. (S.F. Snieszko, ed.). American Fisheries Society, Washington, D.C., Special Publication 5: 177—189.
Menzies, R.J. & W.L. Kruczynski, 1983. Isopoda Crustacea (exclusive of Epicaridea). Memoirs of the *Hourglass* Cruises 6: 1—126.
Miers, E.J., 1876. Catalogue of the stalk and sessile-eyed Crustacea of New Zealand. Colonial Museum and Geological Department of New Zealand, National History Publication 10: i—xii, 1—133.
——— 1877. On a collection of Crustacea, Decapoda and Isopoda, chiefly from South America, with descriptions of new species. Proceedings of the Zoological Society, London 43: 653—679, pls 66—69.
——— 1880. On a collection of Crustacea from the Malaysian Region — Part IV. Penaeidae, Stomatopoda, Isopoda, Suctoria, and Xiphosura. Annals and Magazine of Natural History 5 series 5: 457—467.
——— 1884. Crustacea. **In** 'Report of the Zoological collections made in the Indo-Pacific Ocean during the voyage of HMS 'Alert', 1881-1882'. Isopoda. pp. 299-311. British Museum (Natural History), London.
Milne Edwards, H., 1840. Histoire naturelle des Crustacés comprenent l'anatomie la physiologie et la classification de ces animaux. III. 605 pp.
Monod, T., 1923a. Notes carcinologiques (Parasites et Commensaux). Bulletin de l'Institut Océanographique de Monaco 427: 1—23.
——— 1923b. Prodrome d'une faune Tanaidacea et des Isopoda (excl. Epicaridea) de côtes de France (exc. Mediterranee). Annales de la Société des Sciences Naturelles de la Charante-Inférieure (La Rochelle) 37: 19—124.
——— 1924. Parasitologia Mauritanica. Materiaux pour la faune parasitologique en Mauretanie. Fascicule 1, Deuxieme partie. Isopoda. Bulletin du Comité d'Étude Historiques et Scientifiques de l'Afrique Occidentale Française 9: 67—84.
——— 1931. Sur quelques crustacés aquatiques d'Afrique (Cameroun et Congo). Revue de Zoologie et de Botanique Africaine 21: 1—36.
——— 1934. Isopodes marins des campagnes du "de Lanessan". Notes de l'Institute Océanographique de l'Indochine, Saigon 23: 1—22, pls 1—45.
——— 1976. Expédition Rumphius II (1975). Crustacés parasites, commensaux, etc. (T. Monod et R. Serène, ed.). III. Crustacés Isopodes (1re partie: Corallanidae, Anilocridae, Cymothoidae). Bulletin du Muséum National d'Histoire Naturelle, 3 série, 391, Zoologie 273: 853—870.
Montalenti, G., 1948. Note sulla sistematica e la biologia di alcuni Cimotoidi de Golfo di Napoli. Archivo di Oceanografia e Limnologie, Venice 5: 26—81, pls 1—8.
Moreira, P.S. & V. Sadowsky, 1979. An annotated bibliography of parasitic Isopoda (Crustacea) of Chondrichthyes. Boletim do Instituto Oceanografico, Sao Paulo 27: 95—152.
Morton, B., 1974. Host specificity and position on the host in *Nerocila phaeopleura* Bleeker (Isopoda, Cymothoidae). Crustaceana 26: 143—148, 1 pl.
Nierstrasz, H.F., 1915. Die Isopoden-Sammlung im Naturhistorischen Reichsmuseum zu Leiden. — 1. Cymothoidae. Zoologische Mededeelingen, Rijksmuseum van Natuurlijke Historie te Leiden 1: 71—108, pls 3, 4.
——— 1918. Alte und neue Isopoden. Zoologische Mededeelingen, Rijksmuseum van Natuurlijke Historie te Leiden 4: 103—142, pls 9, 10.
——— 1931. Die Isopoden der Siboga-Expedition. 3. Isopoda Genuina. 2. Flabellifera. Siboga-Expeditie 32c: 123—233, pls 10, 11.
Nobili, G., 1903. Crostacei di Singapore. Bulletino dei Musei di Zoologia ed Anatomia Comparata della ita di Univers Torino 18(455): 1—39.
Norman, A.M. & T. Scott, 1906. The Crustacea of Devon and Cornwall. W. Wesley & Sons, London, 232 pp.
Nunomura, N., 1981. Isopod crustaceans from Sado Island in the Sea of Japan. Annual Report of the Sado Marine Biological Station, Niigata University 11: 43—62.
O'Connor, P.F., 1978. The biology, life-cycle and host-effects of Isopoda (Cymothoidae) found to parasitise the luderick, *Girella tricuspidata.* Unpublished Masters thesis, University of Sydney.
O'Riordan, C.E., 1983. Marine fauna notes from the National Museum of Ireland — 8. Irish Naturalists Journal 20: 551—553.
Parimala, S., 1984. *Nerocila pigmentata* Bal and Joshi (Isopoda: Cymothoidae) parasitic on *Nematalosa nasus* (Bloch). Journal of the Marine Biological Association of India 21 (1979): 180—181.
Pillai, N.K., 1954. A preliminary note on the Tanaidacea and Isopoda of Travancore. Bulletin of the Central Research Institute, University of Travancore (C) 3: 1—21.
——— 1963. Two new genera of parasitic isopods from Kerala. Journal of the Zoological Society of India 15: 66—72.
*Pelseneer, P., 1886. Note sur la présence de *Caridina Desmaresti* dans les eaux de la Meuse. Bulletin du Muséum Royale d'Histoire Naturelle de Belgique 4: 211—222.
Popov, A.M. von, 1933. Über parasitische isopoden von fischen aus dem Schwarzen Meer. Zoologischer Anzeiger Akademische Verlagsgesellschaft, MBH Leipzig 101: 193—198.
*Preud'homme de Borre, A., 1886. Note sur les Crustacés Isopodes de Belgique. Comptes Rendus de la Société Entomologiqe de Belgique 1886: lxxxiv—lxxxvi, figs.
Ramaskrishna, G. & P. Venkata Ramaniah, 1978. A new cymothoid of the genus *Nerocila* from Madras. Bulletin of the Zoological Survey of India 1: 177—180.
Reichenbach-Klinke, H.H. Heinz-Hermann & M. Landolt. 1973. Fish Pathology. T.F.H. Publications, Hong Kong, 512 pp.
Richardson, H., 1901. Papers from the Hopkins Stanford Galapagos Expedition, 1898—1899. VI. The isopods. Proceedings of the Washington Academy of Sciences 3: 565—568.
——— 1904. Contribution to the natural history of the Isopoda. Proceedings of the United States National Museum 27: 1—89.
——— 1905. A monograph on the isopods of North America. Bulletin of the United States National Museum 54: 1—727.

Richardson, H.S., 1914. No. 8. Reports on the scientific results of the expedition to the tropical Pacific, in charge of Alexander Agassiz, on the U.S. Fish Commission Steamer Albatross, from August, 1899, to March, 1900, Commander Jefferson F. Moser, U.S.N., commanding. XVII. Reports on the scientific results of the expedition to the eastern tropical Pacific in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer Albatross, from October 1904 to March, 1905, Lieut. Commander L.M. Garrett, U.S.N., commanding. XXVIII. Isopoda. Bulletin of the Museum of Comparative Zoology at Harvard College 58: 360—371.

Ringuelet, R., 1947. Anotaciones sobre Copépodos et Isópodos parösitos de peces. Notas del Museo de La Plata, Zoologia 12: 93—107, pls 1, 2.

Risso, A., 1816. Histoire Naturelle des Crustacés des Environs de Nice. Librarie Grecque-Latine-Allemande, Paris. 175 pp, 3 pls.

Rockicki, J., 1981. The ectoparasites (Crustacea and Monogenea) of *Brama raii,* the shelf of north west Africa. Acta Parastologica Polonica, Warsaw 28: 85—90.

———— 1984. Parasitic isopods of the NW African Shelf in connection with their occurrence in fish. Universitet Gdanski. Zeszyty Naukow. Rozprawy: Monografie 50: 1—220 (in Polish).

Romestand, B., 1979. Étude ecophysiologique des parasitoses à cymothoadiens. Annales de Parasitologie (Paris) 54: 423—448, pls 1—4.

Romestand, B., M. Janicot & J.-P. Trilles, 1977. Modifications tissulaires et réactions de defense chez quelques Téleostéens parasitér par les Cymothoidae (Crustacés, Isopodes, Hématophages). Annales de Parasitologie (Paris): 177—180.

Romestand, B. & J.-P. Trilles, 1975. Les relations immunologiques-hôte-parasite chez les Cymothoidae (Isopoda, Flabellifera). Comptes Rendus de l'Acadmie des Sciences, Paris 280: 2171—2173.

Romestand, B., J.-P. Trilles & J.G. Lagarrigue, 1971. Essai pour une systématique biochimique chez les isopodes Cymothoidae. Analyse électrophorétique en gel d'acrylamide des proteins de l'hémolymphe de six espèces. Comptes Rendus Hebdominaire de Séances de l'Academie des Sciences, Paris 272: 447—450.

Roubal, F.R., J. Armitage & K. Rhode, 1983. Taxonomy of metazoan ectoparasites of snapper *Chrysophrys auratus* (Family Sparidae) from southeastern Australia and New Zealand. Australian Journal of Zoology, Supplementary Series 94: 1—68.

Say, T., 1818. An account of the Crustacea of the United States. Journal of the Academy of Natural Sciences, Philadelphia 1: 393—401, 423—433.

Schiödte, J.C. & Fr. Meinert, 1879. Symbolae ad monographium Cymothoarum crustaceorum isopodum familiae. I. Aegidae. Naturhistorisk Tidsskrift Series II, 12: 321—414, pls 7—13.

———— 1881. Symbolae ad monographium Cymothoarum crustaceorum isopodum familiae. II. Anilocridae. Naturhistorisk Tidsskrift Series II, 12: 1—166, pls 1—10.

———— 1883. Symbolae ad monographium cymothoarum crustaceorum familiae. III. Saophridae. IV. Ceratothoinae. Naturhistorisk Tidsskrift Series III, 13: 281—378, pls 11—16.

———— 1884. Symbolae ad monographium cymothoarum crustaceorum isopodum familiae. IV. Cymothoidae Trib. II. Cymothoinae. Trib. III. Lironecinae. Naturhistorisk Tidsskrift Series III, 14: 221—454, pls 6—13.

Schuurmans Stekhoven, J.H. Jr., 1937. II. Parasitic isopods. Pp. 25—26 of Crustacea parasitica. **In** 'Résultats scientifiques des croisieres du Navire-École Belge 'Mercator'. Vol. 1. Mémoires du Musée Royal d'Histoire Naturelle de Belgique, Deuxième Série 4: 11—26.

Scott, D., 1964. Parasitic isopods on trout. Proceedings of the New Zealand Ecological Society 11: 23.

Serène, R., 1937. Inventaire des Invertebrés marins de l'Indochine (1er liste). Notes de l'Institut Océanographique de l'Indochine 30: 1—83.

Southwell, T., 1915. Notes from the Bengal Fisheries Laboratory, Indian Museum. No. 2. On some Indian parasites of fish, with a note on carcinoma in trout. Records of the Indian Museum, Calcutta 11: 311—330, pls 26—28.

Stalio, L., 1877. Catalogo metodico e descrittivo dei Crostacei dell'Adriatico. Atti de Reale Instituto Venetu di Scienze, Lettere ed Arti (5)3: 1345—1387.

Stebbing, T.R.R., 1893. A History of Crustacea. Recent Malacostraca. Kegan Paul and Trench, London. Pp. xvii + 466.

———— 1902. South African Crustacea. Part 2. **In** 'Marine Investigations in South Africa' Volume 2. pp 1—92. Department of Agriculture, Cape Town.

———— 1910. General catalogue of South African Crustacea. Part V of S.A. Crustacea, for the Marine Investigations in South Africa. Annals of the South African Museum 6: 281—594, pls 16—22.

———— 1921. Some Crustacea of Natal. Annals of the Durban Museum 3: 11—26, pls 1—5.

———— 1922. Isopoda and Amphipoda from Angola and South Africa. Goteborgs Kungl vetenskaps - och vitterhets - samhalles Handlingar 25: 1—16, pls i—iv.

———— 1924. Crustacea of Natal. Fisheries and Marine Biological Report No. 3, for the year 1922, 3: 1—15, pls 11—16.

Stossich, M., 1880. Prospetto della fauna de mare Adriatico. Parte III. Bollettino della Societa Adriatica di Scienze Naturale in Trieste 6: 178—271.

Szidat, L., 1955. Beitrage zur Kenntnis der Reliktfauna des La Plata-Stromsystems. Archiv fur Hydrobiologie 51: 209—260.

———— 1956. Der marine charakter der parasitenfauna der susswasserfische des stromsystems des Rio de la Plata und ihre dentung als reliktfauna des Tertiaren Tethys-Meeres. Proceedings of XIV International Congress of Zoology, Copenhagen 1953: 128—138.

———— 1965. Sobre la evolucion del dimorfismo sexual secundario en isopodos parasitos de la familia Cymothoida (Crust. Isop.). Anais do Segundo Congreso Latino-Americano do Zoologia, Sao Paulo, Brazil 1962, 2: 83—87.

Tattersall, W.M., 1905. The marine fauna of the coast of Ireland. Part V. Isopoda. Scientific Investigation, Ministry of Fisheries, Irish Free State (1904), 90 pp, 11 pls.

Teodoro, S., 1972. *Braga bachmanni,* nuevo ectoparasito de *Ancistrus cirrosus* (Crustacea, Cymothoidae en Pisces, Loricariidae). Neotropica 18(57): 141—145.

Thomson, G.M., 1889. Notes on, and recent additions to, the New Zealand crustacean fauna. Transactions of the

New Zealand Institute 21: 259—268.
Thomson, G.M. & C. Chilton, 1886. Critical list of the Crustacea Malacostraca of New Zealand. Transactions of the New Zealand Institute 18: 141—159.
Thuet, P. & B. Romestand, 1981. Les tranferts d'eau en fonction de la salinité du milieu chez deux isopodes Cymothoidae: *Meinertia oestroides* (Risso, 1826) et *Anilocra physodes* (L., 1758) (parasites de poissons marins). Archives Internationales de Physiologie et de Biochemie 89: 15—33.
Trilles, J.-P., 1961. Sur *Nerocila d'Orbignyi* Schiödte et Meinert 1881 (Isopoda, Cymothoidae) de bassin occidental de la Méditerranée. Congrés dès Sociétés Savantes de Montpellier 86, Comptes Rendus 86e: 689—696.
———— 1962. Remarques morphologiques et biologiques sur les "Isopodes Cymothoidae" parasites des poissons, de l'Etang de Thau. Naturalia Monspelogia 3: 101—124.
———— 1963. Evolution de la glande androgène et des gonades chez *Nerocila orbignyi* (Schiödte et Meinert) (Isopoda, Cymothoidae) Note Préliminaire. Bulletin de la Société Zoologique de France 88: 609—612.
———— 1964a. Persistance des glandes androgènes, durant le stade femelle, chez les isopodes Cymothoidae. Interprétations. Comptes Rendus de l'Academie de Sciences, Paris 258: 5989—5991.
———— 1964b. Sur différents aspects du développement de l'ovaire chez les isopodes Cymothoidae et l'existence d'une vittellogenèse aberrante dans les ovocytes de certains de ces parasites. Comptes Rendus de l'Academie de Sciences, Paris 258: 6545—6548.
———— 1964c. Glandes androgènes, gonades et metamerisation chez isopodes, Cymothoidae. Bulletin de l'Institute Océanographique de Monaco 62(1293): 108.
———— 1964d. Specificité parasitaire chez les isopode Cymothoidae Méditerranéens. Note préliminaire. Vie et Milieu 15: 105—116.
———— 1964e. A propos e'un fait particulaire d'éthologie parasitaire chez les isopodes Cymothoidae. La relation de taille entre parasites et poissons. Note préliminaire. Vie et Milieu 15: 365—369.
———— 1964f. Note préliminaire sur quelques aspects de la reproduction chez les isopodes cymothoidae Méditerranée. Archives de Zoologie Éxperimentale et Générale 104: 127—134.
———— 1969. Recherches sur les isopodes "Cymothoidae" des côtes françaises. Aperçu générale et comparatif sur la bionomie et la sexualité de ces crustacés. Bulletin de la Société Zoologique de France 94: 433—445.
———— 1972. Sur quatre isopodes cymothoidés du Pacifique (Nouvelle Caledonie). Cahiers de l'Office de Recherche Scientifiques et Techniques Outre Mers, série Oceanographique 10: 3—17.
———— 1973a. Les Cymothoidae (Isopoda, Flabellifera) des côtes françaises (Systématique, faunistique, écologie et répartition geographique). I. Les Ceratothoinae Schiödte and Meinert, 1883. Bulletin du Muséum National d' Histoire Naturelle, Paris 3e série. 91. Zoologie 70 (1972): 1191—1230.
———— 1973b. Sur la structure des pléopodes et des oostegites chez les Cymothoidae (Isopoda, Falbellifera) et ses rapports avec les caractéristiques ecologiques des espèces. Bulletin du Muséum National d'Histoire Naturelle, Paris 3e série, 91, Zoologie 70 (1972): 1269—1277.
———— 1973c. Notes documentaires sur les isopodes cymothoadiens parasites de poissons d'eau douce de l'Amerique du Sud. Bulletin du Muséum National d'Histoire Naturelle, Paris 3e série, 114, Zoologie 88: 239—272.
———— 1975a. Les Cymothoidae (Isopoda, Flabellifera) des collections du Muséum National d'Histoire Naturelle de Paris. II. Les Anilocridae Schiödte et Meinert, 1881. Genres *Anilocra* Leach, 1818, et *Nerocila* Leach, 1818. Bulletin du Muséum National d'Histoire Naturelle, Paris 3e série, 290, Zoologie 200: 303—340, pls 1, 2.
———— 1975b. Les Cymothoidae (Isopoda, Flabellifera) des côtes françaises. II. Les Anilocridae Schiödte et Meinert, 1881. Genres *Anilocra* Leach, 1818, et *Nerocila* Leach, 1818. Bulletin du Muséum National d'Histoire Naturelle, Paris 3e série, 290, Zoologie 200: 347—378, pl. 1.
———— 1975c. Les Cymothoidae (Isopoda, Flabellifera) des collections du Muséum national d'Histoire naturelle de Paris. III. Les Cymothoinae Schiödte et Meinert, 1884. Genre *Cymothoa* Fabricius, 1787. Bulletin du Muséum National d'Histoire Naturelle, Paris 3e série, 318, Zoologie 225: 977—993.
———— 1977. Les Cymothoidae (Isopoda, Flabellifera; parasites de poissons) du Rijksmuseum van Natuurlijke Historie de Leiden. Méditerranée et Atlantique nord-orientale. Zoologische Mededelingen, Rijksmuseum van Natuurlijke Historie te Leiden 52: 7—17.
———— 1979. Les Cymothoidae (Isopoda, Flabellifera; parasites de poissons) du Rijksmuseum van Natuurlijke Historie de Leiden II. Afrique, Amerique et regions Indo-Ouest-Pacifique. Zoologische Mededeelingen, Rijksmuseum van Natuurlijke Historie te Leiden 54: 245—275.
———— 1986. Les Cymothoidae (Crustacea, Isopoda, Flabellifera) d'Afrique. Bulletin du Muséum National d'Histoire Naturelle, Paris 4e série, 8, section A: 617—636.
Trilles, J.-P. & I. Paperna. 1980. Sur quelques Crustacés Isopodes (Corallanidae, Lironecinae et Anilocridae) d'Israel. Bulletin du Muséum Nationale d'Histoire Naturelle, Paris 4e serie, 2 section A: 445—454.
Trilles, J.-P. & A. Raibaut, 1971. Aegidae et Cymothoidae parasites de poissons de Mer Tunisiens: Premier resultad. Bulletin, Institut National, Scientifique et Technique d'Océanographie et de Peche, Salambo 2: 71—86.
———— 1973. Sur les Cymothoidae (Isopoda, Flabellifera) parasites de poissons marins de Tunisie (2e note). Bulletin du Muséum National d'Histoire Naturelle, Paris 3e serie, 114, Zoologie 88: 273—287.
Van Name, W.G., 1920. Isopods collected by the American Museum Congo Expedition. Bulletin of the American Museum of Natural History 43: 42—108.
———— 1936. The american land and fresh-water isopod Crustacea. Bulletin of the American Museum of Natural History 71: 1—535.
———— 1940. A supplement of the american land and fresh-water isopod Crustacea. Bulletin of the American Museum of Natural History 77: 109—142.
White, A., 1847. List of the Specimens of Crustacea in the collection of the British Museum. British Museum, London, pp vii + 143.

White, A. & E. Doubleday, 1843. **In** E. Dieffenbach 'Travels in New Zealand; with contributions to the Geography, Geology, Botany and Natural History of that Country'. Vol. II pp. iv + 396. John Murray, London.

Whitelegge, T., 1902. Crustacea. Part II. Isopoda. Part I. **In** 'Scientific Results of the Trawling Expedition of HMCS "Thetis", Vol. I'. Memoirs of the Australian Museum 4: 201—246.

Williams, E.H. Jr. & L.B. Williams, 1980. Four new species of *Renocila* (Isopoda: Cymothoidae), the first reported from the New World. Proceedings of the Biological Society of Washington 93: 573—592.

——— 1981. Nine new species of *Anilocra* (Crustacea: Isopoda: Cymothoidae) external parasites of West Indian coral reef fishes. Proceedings of the Biological Society of Washington 94: 1005—1047.

Wunder, S.W., 1962. *Nerocila orbignyi,* ein protandrischer hermaphrodit und parasitischer isopode auf *Tilapia galilaea* im see Borullus in Egypten. Verhandlungen der Deutschen Zoologischen Gesellschaft 22: 140—151.

Zirwas, C., 1911. Die isopoden der Nordsee. Wissenschafdliche Meeresuntersuchungen ´der Komission zur wissenschaftlichen Untersuchung der deutschen Meere Zwolfter Band 12: 73—118.

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